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DECEMBER, 1950

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NOTES ON THE BIOLOGY AND SOCIAL BEHAVIOR OF THE ARCHAIC PONERINE ANTS OF THE GENERA MYRMECIA AND PROMYRMECIA

CARYL P. HASKINS AND EDNA F. HASKINS

Few groups of ants are so potentially interesting to the myrmecologist primarily concerned with phylogeny and social behavior in the Formicidae as the extraordinarily archaic ponerine tribe Myrmecii, composed of the large-eyed, generalized, actively stinging members of the genera *Myrmecia* and *Promyrmecia*. Yet despite the fact that the group has been known and recognized scientifically at least since the beginning of the last century, and despite the striking habitus of many species, very few extensive studies have been made on them outside those of Wheeler and of Clark.

There can be little doubt that the Myrmecii, together with one or two other tribes of ponerine ants such as the Amblyoponii and a few scattered genera among the Cerapachyinae, represent the closest approximation among living ants to the ancestral stirps of the Formicidae. Of these only the Myrmecii are so little specialized to subterranean habits, and retain so many features of structure and habit that are strongly suggestive of more generalized epigaeic solitary aculeates. Careful studies of social organization within such a group, both in the field and in the artificial nest, can hardly fail to be rewarding.

There seem to be few published studies of *Myrmecia* and *Promyrmecia* in the artificial nest to supplement the picture of their social organization obtained in the field. Wheeler was obliged to confine his studies of behavior very largely to the period of two expeditions to Australia, one made in 1914 and the other in 1931, which allowed little time for other than field work. Clark and his colleagues, while they have made numerous and striking observations upon the Myrmecii in the artificial nest over a long period, have not published correlations of these, so far as we are aware, and have necessarily been too thoroughly occupied with the task of constructing a logical taxonomy for the group, heretofore badly confused, to leave as much time for observational work as they would have wished.

Because of this dearth of published material upon the social behavior and habits of *Myrmecia* and *Promyrmecia*, it seemed desirable that

further work be undertaken. The present paper constitutes a very preliminary report upon some of the opening phases of such a program, made at this time in the hope that it may stimulate other students to work with these exceedingly interesting and, in many respects, uniquely significant forms. The work reported includes the results of three years of observation of several species in the artificial nest, including *Promyrmecia pilosula* F. Smith, *P. piliventris* F. Smith, *P. mandibularis* F. Smith, and *P. swalei* Crawley, *Myrmecia forficata* Fabricius, *M. gulosa* Fabricius, *M. vindex* F. Smith, *M. regularis* Crawley, *M. tarsata* F. Smith, and *M. nigrocincta* F. Smith. This laboratory activity was supplemented by four months of observation in the field in Australia, spanning most of a summer and including work in the Northern Territory, Queensland, New South Wales, Victoria, and West Australia. In addition to the species listed above, field observations were also made on *Myrmecia auriventris* Mayr in Queensland, *M. simillima* and *M. forceps* in New South Wales, and *M. nigriceps* in West Australia. This represented the total experience of the authors with the Myrmecii, but the work was undertaken against a background of some twenty-five years of study of the social structure of certain other archaic ponerines, especially the Amblyoponii, in the field and in the artificial nest.

BACKGROUND

The closely related genera *Myrmecia* and *Promyrmecia* form compact natural groups, showing intimate relationships among themselves but set widely apart, both in structure and in habit, from any other living Formicidae. Their closest affiliations are probably with the primitive and generalized fossil genus *Prionomyrmex*, first found by Mayr in the Oligocone Baltic amber, and subsequently more thoroughly studied by Wheeler, and with the living but extraordinarily archaic genus *Nothomyrmecia* described by Clark (1934a). *Myrmecia* and *Promyrmecia* are more specialized than *Prionomyrex* in a number of characteristics, especially in the structure of the peduncular node and the mandibles. Like *Prionomyrmex*, however, they are large-eyed, long-legged, long-bodied insects, pronouncedly suggesting in their general form the lower solitary vespoid types from which ants as a whole were presumably derived. In *Myrmecia* and *Promyrmecia* this resemblance to the lower solitary vespoid stocks is pronouncedly emphasized by the behavior and general habits of the insects. In their incessant restless activity, in their extreme agility and rapidity of motion, in their keen vision and predominant dependence on that sense, in their aggressiveness and proneness to use the powerful sting upon slight provocation, the workers of many species of *Myrmecia* and *Promyrmecia* show more striking superficial resemblances to certain of the Myrmosidae or Multillidae than they do to higher ants.

The Myrmecii are entirely confined in present-day distribution to the Australian continental land mass, to certain of the immediately adjacent small islands, and to Tasmania. There can be little doubt that they represent a relict fauna once of far wider distribution. They are most numerous both in species and in individuals in the cooler portions of the continent from central Queensland around the coast to the middle latitudes of West Australia, in areas where the annual rainfall is

greater than 25 inches. In the northern portion of the continent the group seems to have been largely displaced by an immigrant fauna of predominantly Papuan affiliations. Only a few species of *Myrmecia*, including perhaps *M. nigrocincta*, *M. mjobergi* and *M. auriventris*, are predominantly tropical in distribution. No species of *Myrmecia* or *Promyrmecia* have been reported from the Northern Territory. Two workers, probably of *M. simillima*, were found dead near Darwin in the course of the present study, but the significance of their occurrence there is uncertain. No living forms were found. In the center of the continent, and in areas where the annual rainfall is 15 inches or less, only a single species, the xerophytically specialized *M. desertorum*, occurs to any extent.

With a single exception, all the known forms of *Myrmecia* and *Promyrmecia* are terrestrial in habit. Some of the more timid species occupy small nests, which contain but few individuals, placed in protected situations, and the single or multiple entrances show little or no external earth. Many species, however, form striking nests in prominent situations, exposed to full sunlight and adorned with conspicuous craters or mounds composed of excavated earth with or without an additional "thatch" of loose soil, vegetable debris, or coarse gravel carried to the site from some distance. The entrances of such nests may be single or multiple. In many cases such passages are very large, sometimes attaining a diameter of two inches or more. The nests of the larger species are not infrequently three feet or more in depth, and if excavated in hard or stony soil or among tree roots or large boulders may be almost impossible to explore fully.

The Myrmecii are composed, for the most part, of ants of medium to large size, usually conspicuously colored in black, red, or yellow, and often with striking sculpture or pubescence. In length they range from 5–8 mm. in the workers of *P. pumilio* and *P. infima* to as much as 35 mm. (including mandibles) in the largest workers of *P. eudoxia*. There is relatively little quantitative differentiation between perfect females and workers. The males are pronouncedly wasplike in general form.

The large size, striking coloration, pronounced aggressiveness, and relative abundance of a number of species of *Myrmecia* make them among the most conspicuous features of the biota and ensured that they should be early recognized. *Myrmecia forficata* was described by Fabricius in 1787 from collections made by Sir Joseph Banks in Tasmania. Further species were described about 1850 and subsequently by F. Smith, and by Roger and Mayr as early as 1862. Forel, Emery, Crawley, Viehmeyer, Kirby, and Santschi have all made later contributions to the taxonomy of the Myrmecii. Tepper (1882) gave a striking account of the nuptial flight of one species (probably *M. pyriformis*). Frogatt published on *Myrmecia forficata*, *M. gulosa*, *M. tarsata*, and *M. nigrocincta* in 1905, while Barker (1903) recorded field observations on *M. forficata* and *M. nigrocincta* in Victoria.

By far the most comprehensive publications and research on the phylogenetic, the ecological, and the social aspects of the Myrmecii, however, have been those of Clark (1925a, 1925b, 1927, 1928, 1934a, 1934b, 1943) and of Wheeler (1916, 1932, 1933). Clark, in addition to

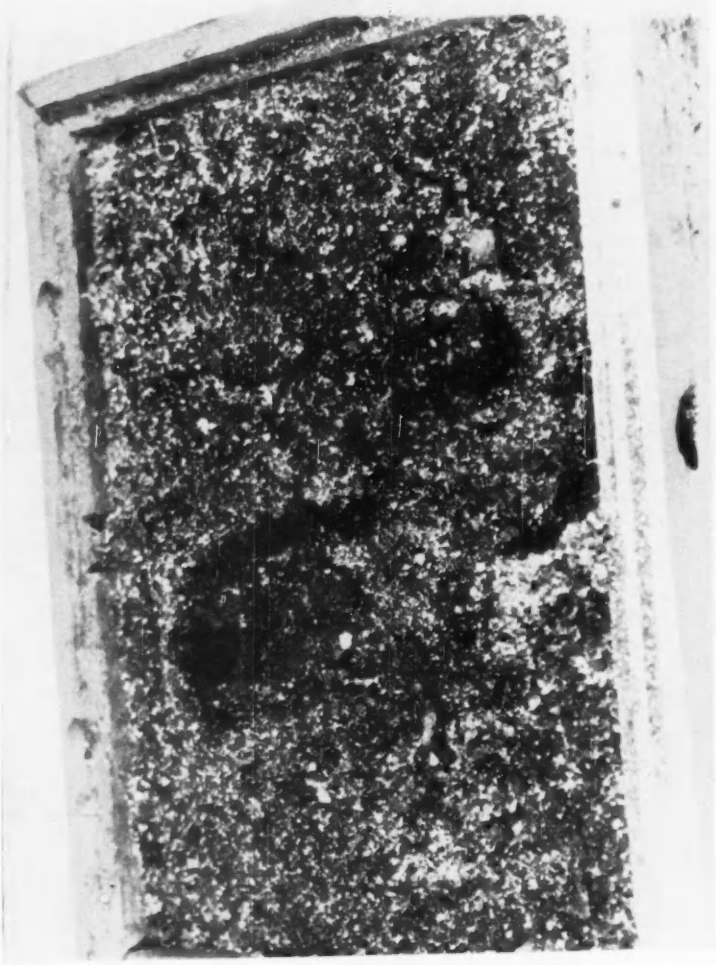

FIG. 1. *Myrmecia regularis*. Initial chamber of colony-founding female.

publishing excellent general habit notes of several species, also described the nuptial flight and the general method of colony foundation in certain of them—a subject of very great importance to an understanding of the origins of social life among the Formicidae. Wheeler, in addition to his very great contributions to our knowledge of the behavior of the Myrmecii in general, was the first to fully outline the concept of an intermittently claustral method of colony foundation, earlier suggested and described by Clark, and to point out its very great significance as an evolutionary step in the development of formicid societies. This concept is of major significance. It will be expanded below, and confirmatory data will be presented.

General Features of Colonial Structure

The colonies of most species of *Myrmecia* and *Promyrmecia* contain but a single fertile female, far less strikingly differentiated from the worker caste than is usual in the higher Formicidae. In a few species, however, the colonies may be pleometrotic. This is notably true of *Promyrmecia pilosula* in which Wheeler (1933) reported finding as many as four females in a single colony. This was amply confirmed in the present study. Thus, of eight colonies of the species examined at Mt. Kosciusko, seven contained more than one fertile female and one contained no less than thirteen. The fertile females from this colony, housed in the artificial nest, have continued to co-operate actively in colonial functions for more than a year.

The eggs of the Myrmecii are proportionately large, varying from about 1 mm. to 1.5 mm. in the longer axis. Unlike those of other ants, they are subspherical in form, and, in most species, are not agglomerated into packets, but lie scattered singly in the brood-chambers. In *P. pilosula* and possibly a few other species, there is occasionally some indication of the formation of an egg packet, so characteristic in the higher ants. When the nest is disturbed, each egg is carried away to safety individually by the active and aggressive workers.

The young larvae, in contrast to the eggs, are markedly adhesive, and during earlier instars are agglomerated into packets. The larvae are fed with pieces of whole insects, brought into the formicary by foraging workers and distributed among them. The adults among all the Myrmecii are highly nectarivorous in habit. Insect food is taken by adult workers, but only rarely and sparingly when larval brood is not present in the nest, and little or no insect food is brought into the formicary at this time. As soon as young larvae have appeared, however, the change in the food habits of the adults is very striking. Insect food is now taken extensively, and, among the more active species, a constant stream of prey pours into the nest, to be avidly licked by the nurses and distributed among the larvae. As soon as the majority of the larvae become enclosed in cocoons, the food habits are again abruptly shifted. The co-ordination is not absolute, but is strikingly close in many species.

The pupae of all known species of the Myrmecii are enclosed in cocoons, which are usually thick and tough but do not differ markedly in structure or appearance from those of higher ants. They are stacked and tended by the adult nurses as among the higher ants. In their

FIG. 2. *Myrmecia vindex*. Colony-founding female in initial chamber.

manner of eclosion these cocoons differ significantly from those of higher ants, in a manner to be discussed below.

Such is the very general character of colonial structure among the Myrmecii. Superficially it is not strikingly different from that which obtains among higher ants. It is in what might be called the "fine structure" of colonial organization and behavior that differences of great interest, and probably of great evolutionary significance, appear. A number of these will be discussed below.

RELATIONS BETWEEN ADULTS, AND BETWEEN ADULTS AND YOUNG

In no group of ants, perhaps, are the social relations among the members of the colony at a more primitive level than among the Myrmecii. An equal simplicity is to be found in the Amblyoponii and among some of the Cerapachyinae, but in the Myrmecii alone extreme simplicity of basic colonial structure is combined with a rather high degree of over-all colonial organization apparently at variance with it.

It is characteristic of all the known species of *Myrmecia* and *Promyrmecia* that regurgitation of the ingluvial contents of the crop is impossible in the adult female and worker. This situation not only precludes ingluvial feeding of the larvae, so universal among higher ants, but also makes any direct exchange of nutriment among adults an impossibility. Only two cases have been seen among hundreds of observations made in the artificial nest in which there was any indication of the power to regurgitate. In one instance a worker of *M.* tarsata, grasped by the thorax with forceps when full-fed with honey, exuded a droplet on the labrum. In the other, a worker of *P. pilosula* (with little doubt the most highly socially organized species of the Myrmecii) was observed in the artificial nest to align itself with an individual which had been feeding on dilute honey and to avidly lick its mouthparts. It seems likely, however, that this movement did not involve regurgitation of crop contents, but was simply designed to avail the solicitor of excess honey adhering to the mouthparts of the feeding individual. With these two dubious exceptions, no evidence of the possibility of transfer of food from individual to individual has ever been detected.

The phenomenon of trophallaxis, first defined by Wheeler (1910), and, as he pointed out, one of the most powerful social bonds among higher ants, is thus largely wanting among the Myrmecii. It should be added, however, that the larvae apparently produce abundant dermal exudates when fed insect food, as do those of the higher ants, and these are avidly licked by the adults. This licking of the larvae commences almost immediately after they are hatched and is continued throughout larval life. It has been observed in the artificial nest in colonies of all the species examined, and among isolated colony-founding females with their very young broods in *Myrmecia forficata* and *M. vindex*. It is peculiarly interesting that the characteristic "soliciting" movement of the forelegs, closely associated with the supplication for ingluvial food among adults of the higher ants, is also well developed in *Myrmecia* and *Promyrmecia*, but here appears predominantly when adults are rasping the larvae for exudates. It thus appears, among these socially primitive forms, to be only a general excitatory reaction

without specific social significance. This conclusion is of interest in view of the very similar interpretation of Maier and Schneirla (1935, p. 171) of the corresponding movements in very young callows of the higher ants, before they have taken on stereotyped social implications and functions. It is also of interest that adults, when licking the larvae, characteristically pinch and pull them, especially about the thoracic segments, in an evident effort to assist the flow of exudates—a procedure strikingly reminiscent of the habit among the nurses of such primitive social vespine genera as *Polistes* of pulling the larvae half way out of their cells and jamming them back, in an attempt to stimulate the salivary flow. This procedure of pinching has been seen even among colony-founding females of *Myrmecia forficata*, applied to very young larvae apparently far too fragile to endure such treatment.

It follows from these observations that the relationship between adults and young, as well as among adults, is far less stereotyped, far less socially evolved, and far less finely "modulated" among the Myrmecii than is the case among the higher ants. Thus the larvae, although licked and attended fairly continuously, often make their own way largely unassisted to the insect prey which is brought in by the nurses and scattered among them, and feed on it as opportunity offers, after the manner of the larvae of solitary sphecoids feeding on the paralyzed prey which has been left with them. The larvae of *Myrmecia* and *Promyrmecia* possess unusually well-developed body musculature and powerful mandibles, and have considerable powers of movement. They often attack, and not infrequently kill and devour, one another, especially when insect prey is scarce, and they have been seen to attack the adult nurses in the artificial nest.

The most finely adjusted behavioral patterns between adults and young are probably those which obtain at the time of the spinning of the cocoon by the larva on the one hand, and the eclosion of the pupa on the other. At the time that the larva is ready to spin the cocoon, it is regularly covered rather thickly with earth by its nurses, the particles of debris serving as anchor-points for the silk. This "banking" process is critical in the life of the larvae, for if it is neglected no cocoon can be spun and the young ordinarily perish. The process has been observed, under natural conditions or in the artificial nest, in many species, including *M. tarsata*, *M. gulosa*, *M. forceps*, *M. vindex*, *M. nigrocincta*, *P. piliventris*, and *P. pilosula*. As soon as the cocoon has been completed, it is removed and cleaned by the adults so that, in most species, no earth particles are left adherent. Among some species, which frequently nest in pure sand, however, notably *M. vindex*, this cleaning is very imperfect, and the cocoon is characteristically thickly studded with silica granules.

In the behavior of the adults toward the cocoon at the time of eclosion of the pupa, the Myrmecii exhibit an extremely interesting transitional stage in the evolution of intracolonial relationships. Among higher ants, the habit of adult workers of rendering extensive assistance to the young individual in escaping from the cocoon is so firmly fixed that without it the pupa is unable to emerge. Typically, among formicine ants, the cocoon is opened from the outside, the pupa is extracted before the pupal skin is shed, the skin is subsequently removed

by the attendant nurses, and the wings of the sexual forms are expanded. The young insects are extremely soft, callow, and helpless when first eclosed and it is usually several days before they harden and become capable of much movement. The work of Schneirla and others has indicated that it is predominantly during this relatively quescent period that many "learned" reactions are acquired and fixed which fit the young individual more perfectly to its social environment.

Among such socially primitive forms as the Amblyoponii the situation is almost exactly opposite. The pupal skin of the emerging adult is shed within the cocoon, the wings, if it is a sexual form, are expanded, and only thereafter the young insect itself gnaws open the cocoon and emerges. Characteristically, the young males are fully pigmented on emergence and capable of leaving the nest to fly within a few hours, and the young perfect females and workers, although somewhat callow, are able to assume active colonial duties almost immediately. Thus, incidentally, the only period of the life of the adult in which "plastic" adjustments of the individual to its social environment occur at all readily is passed in the cocoon by the young workers of the Amblyoponii, and, in a social sense, is "wasted." This situation was reported by Wheeler in *Stigmatomma pallipes* many years ago and has been amply confirmed by the authors in this species (1928) and more recently in *Amblyopone australis*.

The situation in *Myrmecia* and *Promyrmecia* in this respect has long been uncertain. It has been an open question whether young members of the colony normally emerge from the cocoon without active assistance from the workers, and whether they emerge in a callow or in a fully pigmented condition. Observations made in the course of this study on *Promyrmecia pilosula* and *P. piliventris* and *Myrmecia forficata* and *M. vindex* appear to give a definitive answer, at least for these species, and to indicate a most interesting state of transition in this aspect of intracolonial relationships.

Numerous cocoons of *P. pilosula* were isolated shortly before they were due to hatch. Some of these had been collected in the wild, others were from larvae reared in the artificial nest. The course of development was the same in all cases. Eclosion was delayed beyond the usual time, the pupal skin of the young imago was shed in the cocoon, and the adult advanced to full pigmentation and full activity. At this time, strenuous efforts were begun to escape from the cocoon. A hole was made and the mandibles were extruded. As soon as this happened, however, further progress became difficult since the cutting edges of the long specialized mandibles no longer made efficient contact with the cocoon. At this stage, about half of the individuals failed to progress further and ultimately perished. The remainder emerged successfully. They were fully pigmented and essentially adult. Cocoons of *M. forficata* similarly isolated uniformly failed to produce emergence, although a female of *M. vindex* succeeded in escaping without assistance.

It seems clear that such independent eclosion, though sometimes possible, is not the typical course. This was first indicated by the high proportion of extremely callow individuals found in the nests of all the species of *Myrmecia* and *Promyrmecia* examined at the appropriate

season, including *P. pilosula*—individuals in a far less developed state than those emerging from *P. pilosula* cocoons held in isolation. Observations of the behavior of the nurses of *P. pilosula* with cocoons undergoing eclosion in the artficial nest disclosed what appears to be the normal eclosion process, at least in this species. At the time that the cocoon is ready for eclosion, pupal movements excite the nurses and draw their attention to it. They cluster about the anterior pole, pulling and biting at it. At the same time, the mandibles of the young ant make a small hole and protrude through it. As soon as this occurs, the mandibles are seized by the attendant workers, and, using this projection as a brace, the cocoon is quickly torn away and the young ant is extratced by the nurses and licked profusely. Though callow, the pupal skin has already been shed, and the young adult is ready to assume colonial functions in a relatively shorter time than among the higher ants, though considerably longer than with the Amblyoponii. The Myrmecii, therefore, seem to be intermediate in this respect between the independent hatching characteristic of *Stigmatomma* and *Amblyopone* (where, nevertheless, the nurses commonly pay great attention to the cocoon undergoing eclosion and may occasionally open it, although their services are not required) and the obligatory dependence of the young emerging individual on its nurses which seems to be universal among all the higher ants with enclosed pupae.

It is interesting that, both in *Myrmecia* and *Promyrmecia*, the adjustments between adults and young inherent both in the banking of the larvae preparatory to spinning and in the release of the young imago appear to be much more labile and susceptible to disturbing influences of the outside environment than in higher ants. Thus, in the artificial nest, it is very usual for nurses of species of both *Myrmecia* and *Promyrmecia* to fail to bank the larvae at the proper time, even though they have successfully reared them from the egg, and to destroy the naked semipupae when these are formed. Similarly, it was very common, among all the species studied in the artificial nest, for nurses to cut open healthy cocoons prematurely and to extract the not yet mature pupae and destroy them. So troublesome did this become in several colonies that special precautions were necessary to ensure the rearing of normal broods.

As already indicated, relations among adults in *Myrmecia* and *Promyrmecia* are more tenuous and crude than among the larvae. Deportation of adult workers by other workers is very rarely seen. When it is undertaken, it is an awkward affair, without any standardized form, very unlike the sterotyped pattern of behavior common among the higher ants. Such deportation has never been observed outside of the artificial nest, and here it has been confined to aged or ailing individuals, so that it is questionable whether it ever occurs normally. It has not been seen in continuous observations of populous and thriving colonies of *Myrmecia tarsata* and *M. nigrocincta* in the artificial nest, observations extending in aggregate over two years, nor has it been detected in undisturbed colonies in the field.

Deportation of males, of young callow workers, and of old dealate females, however, does occur occasionally when the nest is disturbed. The deported individual is normally grasped by the mandibles or, in

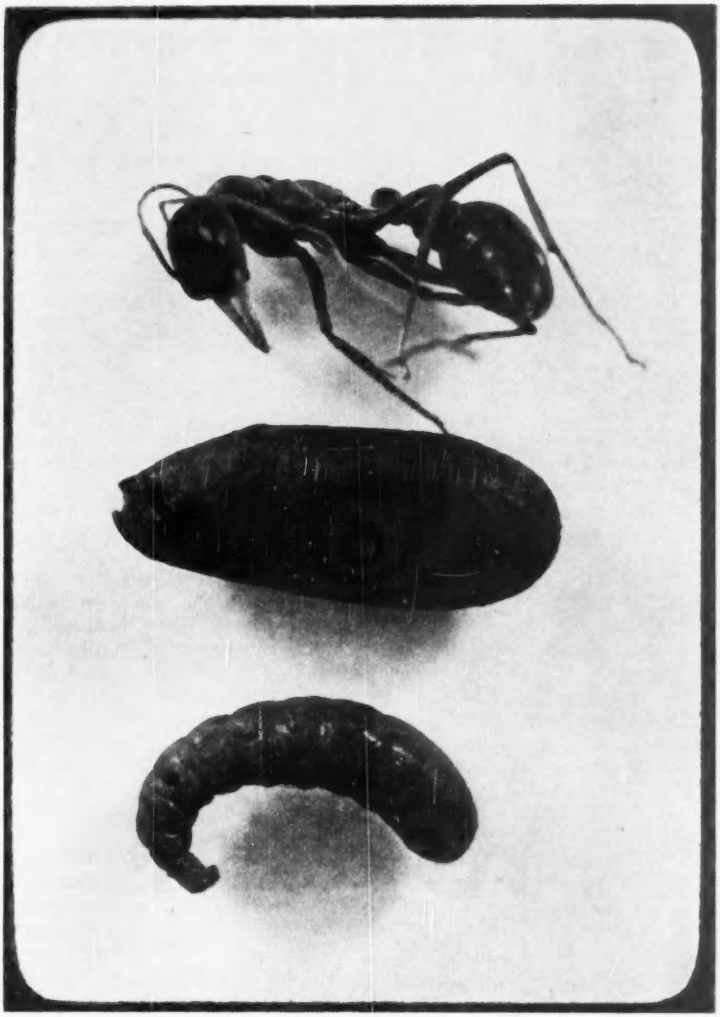

FIG. 3. *Promyrmecia pilosula.* Adult worker, cocoon, and larva.

the case of males, by the antennae, and pulled forward, the deporting individual running backward. The deported individual is never lifted from the ground, and shows no evidence of the tonic immobility or the standardized "deportation attitude" so characteristic of many species of higher ants. It is dragged, often with much resistance, to shelter.

PATTERNS OF COMMUNICATION AND OF FORAGING

The exceedingly low degree of inter-reaction among adult workers of the Myrmecii and the absence of the habit of exchange of ingluvial food lends a curious crudity to inter-individual relationships and to the foraging pattern. Within the nest, adult individuals occasionally rasp one another for surface accumulations, and this may take place upon any part of the body, including the mouthparts. During this time the excitatory motion of the forelegs is in evidence, but has none of the solicitory significance that it carries in higher ants. The individual being rasped becomes immobile during the process. This is essentially the only intimate relation between adults that has been observed in the field or in the artificial nest. All other behavior of the workers seems to be of purely individual character.

During the time that larvae are absent in the formicary, the adults are predominantly nectarivorous, as mentioned above, and little or no insect food is brought within the nest. At such times, individual workers forage alone for nectar, and do not tend particularly to return to the nest when the crop is filled. In this, as in other aspects of foraging behavior, the pattern is in the sharpest possible contrast to that of virtually all the higher ants. When larvae are present, the workers forage individually for insects and other arthropods, and, among the larger species, occasionally for larger forms of life. These are caught with much rapidity and dexterity (honeybees, for example, are a favorite prey of *M. gulosa* near Sydney and other large ants are frequently taken), are paralyzed or killed with the sting, and are promptly brought within the formicary. Here they are deposited near the brood, and licked briefly before the workers again set out for additional prey. No co-operation between individuals in securing insect prey has ever been seen in the field or in the artificial nest. Food particles from which all available nourishment has been secured are carried to the kitchen middens by any individual that happens to be near.

The total lack of co-operation in foraging was well illustrated in a series of experiments conducted both in the field and in the artificial nest. Those in the field were typical. Two populous colonies of *Myrmecia gulosa* were selected for the work, located near Sutherland, N. S. W. The work was done on January 12 and 13, 1948, at a time when most of the brood of these colonies was in larval form and seasonal foraging was at its height. Observations during the two days were begun in the morning, at 10:55 a. m. and 10:15 a. m. respectively, and continued until late afternoon, respectively 4:20 p. m. and 4:00 p. m. The air temperature at the beginning of the first day was 17.0° C., and within the mounds, six inches below the surface of the soil, was 17.5° C. It rose toward noon and then slowly decreased, reaching a low point of 16.0° C. of air temperature (although the nest temperature was 20° C.) at the end of the second day, when the sky was overcast and rain had

begun. During these periods, individual ants in a continuous stream were leaving on foraging expeditions over a half-mile radius about the nests, and were returning laden with insect prey of all sorts.

The experiment consisted in placing plastic cups filled with a mixture of honey and water thirty inches from the nest craters. These were shortly accidentally discovered by individual workers, which fed at them until the crops were distended. The first six individuals to feed were in each case marked with a small dot of nail polish, the individuals being distinguished by various colors of nail polish and by various positions of the mark. In most cases it was possible to mark such individuals while feeding without disturbing them. When the six

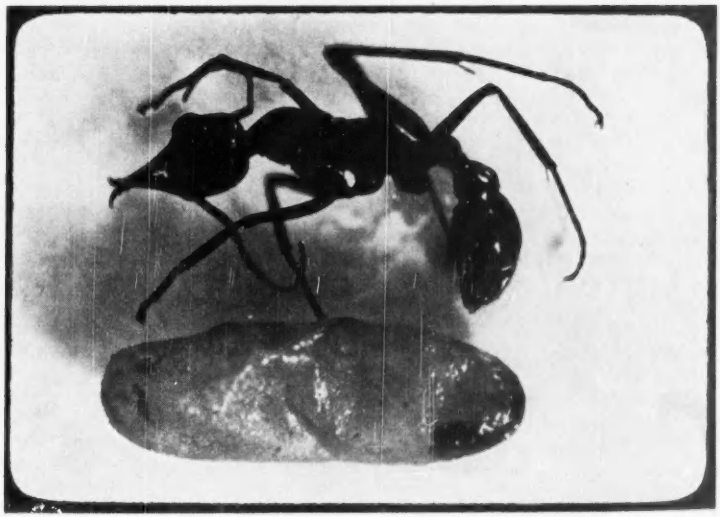

FIG. 4. *Myrmecia nigrocincta*. Adult worker and cocoon.

individuals of each nest had been marked, all ants subsequently finding the honey by chance were imprisoned, and observations made on the marked workers at five- to ten-minute intervals throughout the days.

In all, 132 observations were made of the behavior of such marked individuals in the two nests. The results were singularly stereotyped and uniform. In each case the forager, after feeding, showed no immediate tendency to return to the nest. In somewhat over half the cases, however, it entered the nest within two minutes of feeding. Foragers occasionally remained within the nests after feeding as long as one hour, but usually emerged again within a much shorter interval and returned to feed at the cups. The return was executed rather directly once an initial conditioning had been established. Orientation was evidently accomplished virtually entirely by vision, since the antennae were carried aloft during the whole process. *At no time during the*

entire experiment was a returning forager accompanied by other workers. Nor was there any evidence whatever of a tendency of other workers to follow an odor train to the cup, either of their own or another colony. Unmarked workers which found the honey did so entirely by chance, and were imprisoned. There was not the slightest indication that foraging workers of *M. gulosa* ever guide additional workers to the sites of food that have been discovered—a situation at striking variance with that in the higher ants. There was never even indication of a generalized excitement within the nest caused by the entry of workers which had discovered a particularly rich source of nourishment. Each ant was, in effect, walled off from its fellows. Similar experiments with communities of *M. tarsata* and *M. nigrocincta* in the artificial nest have been confirmatory.

This striking inability to communicate stimuli from one individual to another by any means was, in fact, a prominent characteristic of all the species studied, and probably characterizes the entire group. The Myrmecii do not possess specialized stridulatory mechanisms comparable to such Ponerine genera as *Paraponera* or *Leptogenys*, nor do they set up warning vibrations by any of the numerous secondary means so usual among higher ants, such as striking the walls of chambers and galleries with the head or gaster.[1] This lack of communication was strikingly exhibited when the nests of all the species studied were being excavated. When excavation is begun, workers in the superficial galleries push out excitedly to attack the intruder. The alarm spreads through the nest only very slowly, however, and as each lower chamber is uncovered it is found to be filled with workers which have not yet been aroused by the disturbance above. This situation was particularly evident in excavating the nests of such large species as *Myrmecia vindex*, *M. gulosa*, and *M. tarsata*. It was as true at the height of midsummer foraging activity as at any other time. This is a strikingly different behavior pattern from that of higher ants. If colonies of the larger *Myrmecias* exhibited anything approaching the degree of inter-individual communication or co-ordination common among the higher ants, they would be far more difficult to excavate than is the case.

COLONY RECOGNITION, AND "POLARITY" OF THE COLONY

Colonies of *Myrmecia* and *Promyrmecia*, like those of *Amblyopone* and *Stigmatomma*, are extremely intolerant of the intrusion of alien insects. This intolerance extends to alien members of the same species, which are quickly detected and killed or ejected from the nest. Alien eggs, larvae, or cocoons of the same species are readily accepted, but, unlike the situation among many formicine ants, the adults developing from them are, with very rare exceptions, detected as aliens and expelled within a few hours. Conditioning of workers to the new stimuli presented by alien adults of the same species maturing within the nest

[1]It has been observed, however, that young colony-founding females of *Promyrmecia piliventris* may execute rapid rubbing motions of the second and third gastric segments when excited by food, and careful microscopic examination of the dorsal surface of the third gastric segment near its anterior margin reveals a very slight specialization of the surface contours toward regular striae in that region.

occurs very seldom indeed, whereas it is of course a common phenomenon among higher ants. It is difficult not to speculate whether this phenomenon may be connected with the relatively advanced condition of the adult at the time of hatching from the cocoon, already described.

The situation indeed is more extreme than this. There is considerable evidence that, unless all the members of a given community are in relatively continuous contact, schists will develop so that the members of one portion of the colony may become permanently hostile to the rest. Two interesting bits of evidence concerning this situation were secured.

A large colony of *Myrmecia tarsata*, containing somewhat over five hundred workers and a very large brood, including many sexual pupae, was excavated with its single more or less physogastric brood queen. This queen was isolated, for purposes of transportation, with three adult workers and two cocoons, while a rather large sample of adult workers was placed in a separate container. These two samples were kept isolated for four months, at the end of which period an attempt was made to recombine them in an artificial nest. It was then discovered that, although the fertile female was readily accepted by both groups of workers, the worker groups themselves had become as hostile as though they had been drawn from separate colonies, and remained so permanently. It seems probable that odor played an important part in conditioning this reaction, as among higher ants. It is not clear from this case, however, whether individual differences of odor, such that each member of the colony must be continuously reconditioned to all of its fellows, are responsible, or whether each individual, in the course of its life-cycle, undergoes progressive odor changes to which its fellows must be continually re-accustomed. In either event, it is remarkable that it seems to be necessary for every ant of a colony of *Myrmecia* to encounter every other colony member fairly frequently if the integrity of the social structure is to be preserved. Such a requirement must put a sharp limit on the size which such communities can attain, and upon the possible degree of ramification of the nest.

The second bit of evidence in this connection strongly suggests that progressive changes in the odor of individuals with advancing age may be important, and that significant changes may occur in less than a month.

A relatively large colony of *Myrmecia nigrocincta*, in which nearly all the brood had already matured, was excavated, with its fertile brood-queen. As in the previous case, this queen was isolated with some ten mature workers for transportation, the remainder being placed in a separate container. Two weeks later the workers were colonized in an artificial nest, and the fertile female with the ten attendant workers were introduced. It was then found that the workers already within the formicary now reacted hostilely to the ten workers and to the fertile female, with both of which they had consorted amicably less than fifteen days previously. Both the fertile female and the workers were quickly killed by the remaining colony personnel. It should be added that, both in this instance and in the preceding one, the isolated colony fragments were treated with great care, and that particular precautions were taken not to contaminate either fraction with foreign odors (as by handling) either during the period of separation or at reunion.

Thus it seems evident that a mature community of *Myrmecia tarsata* or *M. nigrocincta* (and probably of other species also) is a more or less constantly inter-communicating body, despite the very low degree of inter-reactivity among its members, and that if barriers to such communication are imposed, the relatively feeble influences which tend to maintain the integrity of a single colony quickly disappear.

SPECIALIZATION OF FUNCTION AND STRUCTURE AMONG WORKERS

Since the Myrmecii possess no means of distributing ingluvial food from one individual to another, nor of storing ingluvial food within the colony, opportunities for any great evolution of specialization of social function among the workers would appear to be sharply limited. During the brood-rearing season, to be sure, a constant supply of insect prey is brought into the nest and is available for the nourishment of adults which may not emerge to forage. The large supplies of larvae, also, serve as a potential source of nourishment through their exudates. This situation creates an ecological "niche" within the colony for a sedentary, non-foraging "nest" caste, such as apparently occurs among so many of the polymorphic higher ants. Among most if not all the Myrmecii, however, this situation is relatively temporary. Foraging for insects, as already indicated, drops off very sharply as the brood is matured, and in the fall and winter almost ceases among many species. It is probable that a few overwintering larvae remain in the nest, but the supply must be small—too small, it may be presumed, to serve as the entire source of nourishment for very many individuals, especially as the destruction and actual devouring of eggs or larvae apparently occurs much more rarely among the Myrmecii than in higher ants. Under such conditions, it would seem imperative that each individual worker leave the nest at intervals to forage for its own sustenance.

This is a difficult matter to test, but experiments with marked individuals of *M. nigrocincta* in the artificial nest have suggested that all the members of a given colony probably do emerge at more or less frequent intervals to seek ingluvial food, although the frequency of emergence varies greatly from individual to individual. It seems improbable that there is any specialized "brood" caste which remains permanently within the nest, or is regularly dependent on food brought in from outside by other foragers.

Consistent with this picture, the workers of most species of *Promyrmecia* are essentially monomorphic in form, and this is true of some species of *Myrmecia*, such as *nigrocincta*. In the majority of *Myrmecia* species, however, the workers exhibit a rather high degree of variability in stature, although very little in terms of bodily proportions. The largest workers may be somewhat more than twice the size of the smallest ones. It is true also that the smallest individuals, on the whole, tend to be less aggressive than the larger ones, and are more often found among the brood pile when the nest is excavated. There are numerous exceptions to this, however, and aggressive smaller individuals have occasionally been found foraging in several species studied in the field.

It is clear that this high degree of variability of worker stature provides a physiological basis for the differentiation of incipient castes. It seemed worth while to investigate more fully the extent to which such

size classes have become segregated to form distinct caste groups in at least one of the larger species of *Myrmecia* which shows typical variability in worker stature. For this purpose, an unusually large colony of *Myrmecia gulosa*, located near Sutherland, N. S. W., was selected, and its worker personnel were collected as completely as possible on

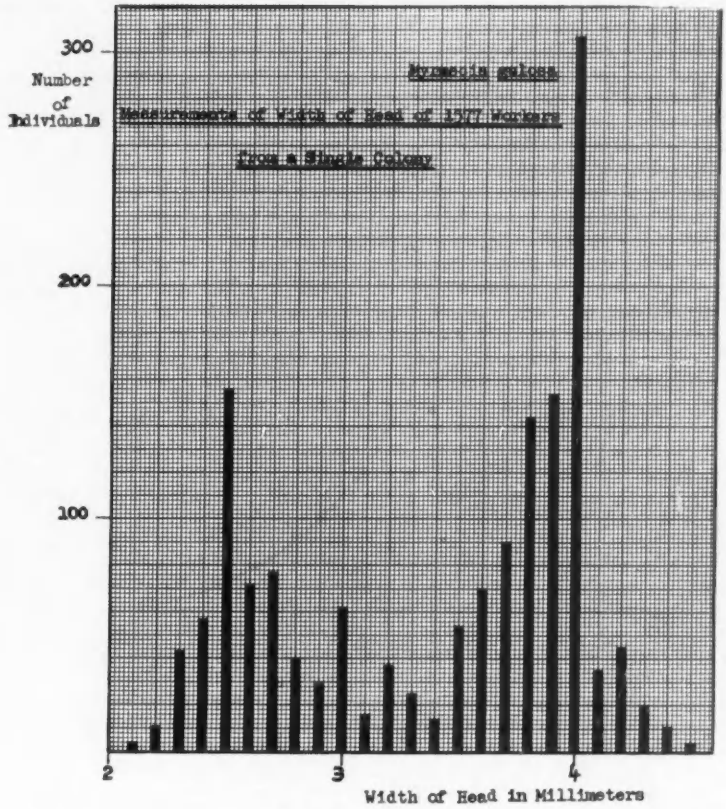

FIG. 5. *Myrmecia gulosa*. Measurements of width of head of 1577 workers from a single colony.

March 22, 1948, near the close of the brood-rearing season. Measurements were taken of the width of the head, viewed dorsally through the points of highest convexity of the compound eyes, of all the workers. This measurement was selected as a practicable criterion of the form and discreteness of size-classes because of the relative uniformity of bodily proportions which is characteristic of *M. gulosa* (as well as other variable species of *Myrmecia*) from workers of smallest to those of

largest stature. It may be added that this colony was one of the two upon which the experiments in communication and foraging behavior described above had been made two months earlier, when it was at the height of its larval-rearing period. During those observations, only members of the larger size-classes had been seen foraging. Several individuals marked with nail polish at that time were found inhabiting the upper galleries and chambers of the nest when it was excavated.

Head measurements were taken of a total of 1577 workers from this colony. The size-classes are shown in the accompanying plot, following the approach used by Weber (1946) and by Cole and Jones (1948) with *Oecophylla*. It will be seen that, in contrast to the situation in that Formicine ant, the size-classes are by no means clearly separated, but overlap very considerably. At the same time, several frequency modes are very clearly evident, suggesting the beginning of an evolution toward polymorphism. Also, the highest peak falls in the region of larger head-size, suggesting that the smaller classes have, in general, been derived from the larger ones that are nearer the stature of the perfect female. It is interesting to speculate whether any further evolution toward polymorphism could take place in the absence of some mechanism for the storage and the distribution of ingluvial food within the nest.

It is interesting further to notice that the variability of stature of the workers of *M. gulosa* seems to be relatively independent of trophic conditions in the colony. Thus the examination of this colony was made at the end of a period of several months during which conditions of temperature and nourishment had been optimum for maximum growth among the larvae. Yet one individual of the very smallest size class obtained (2.2 mm. head width), six of a head width of 2.4 mm., and one of 2.5 mm., were callows newly emerged, indicating that these size classes were probably being produced quite as abundantly, in terms of their normal proportion of the total population, as the larger classes during this optimal period. It seems likely that the causes underlying this variability are basically genetic and physiological rather than nutritional in nature, being related, possibly, to the varying penetrance of gene-complexes characteristic of the species.

NUPTIAL FLIGHT, MODE OF COLONY FOUNDATION, ROLE OF FERTILE FEMALE IN INCIPIENT AND MATURE COLONIES

A vivid description of the nuptial flight in one of the larger species of *Myrmecia* was given as early as 1882 by Tepper in the reference already quoted. It has since been described by Froggatt (1915), by Wheeler (1916), and by Clark (1925–7, 1934a).

The accounts of Tepper, Froggatt, Wheeler, and Clark all refer to the larger species of *Myrmecia*, such as *M. pyriformis*, *M. nigriscapa*, *M. gulosa*, *M. forficata*, and *M. sanginea*, in which the females are fully winged and in which an active flight takes place. The nuptial flight of these species may sometimes occur as a spectacular, "mass" affair, many hundreds of young queens and males emerging simultaneously, and the females being fecundated on bushes or other supports by the active, low-flying males, somewhat after the manner described for *Stigmatomma pallipes* (Haskins, 1928), though far more conspicuously.

It is clear, however, that this pattern of the nuptial flight is not universal in *Myrmecia* and *Promyrmecia*. In a number of forms, such, notably, as the beautiful brown-violet species *Myrmecia regularis* of southwestern Australia, the thorax shows a variable but decided reduction in size, and the wings are abnormally short. This same shortening of the wings obtains among the females of *Myrmecia nigrocincta*, *Promyrmecia piliventris*, and certain other species.

Two series of observations made in the course of the present study strongly indicate that the nuptial flights in such species are aberrant, and that the female, although emerging from the parent colony before fertilization, flies little, or not at all. In the first study, a colony of *Promyrmecia piliventris* in the artificial nest, containing numerous young females and males hatched from cocoons taken in the wild, was returned to the site of capture and opened, permitting the emergence of the winged forms, which shortly took place. It was thus possible to witness an "artificial" nuptial flight, as it were, taking place under essentially natural conditions. A male emerged from this nest in the middle forenoon of January 12, 1948, a clear and sunny day. After running about for a few moments it took flight and disappeared. It was followed by a short-winged female, which exhibited markedly positive phototropism and geotropism and, after running along the ground for a few moments with actively buzzing wings, but without taking flight, mounted a small shrub to its tip. Here, after feeding briefly on the exudates of a colony of aphids, the female became quiet, extending and curving the gaster and rubbing the posterior segments with the hind legs. This pose was maintained for approximately a minute, after which the insect slowly descended to the ground, exhibited reversed phototropism, and was returned to the artificial nest. Although no males appeared, this procedure was so very similar to that described in *Stigmatomma pallipes* (Haskins, 1928) as to strongly suggest that in this species, and probably in others in which the wings of the female are short, fertilization is normally accomplished on the ground or on bushes by the active, low flying males, and the female rarely if ever essays flight. Sisters of this insect, when artificially dealated, founded colonies under laboratory conditions in the manner to be described below.

The situation in *Myrmecia regularis* appears to be even more interesting. It was fortunately possible to thoroughly examine some ten large nests of this species in the magnificent eucalypt forests just south of Manjimup, West Australia—a location almost identical with that where many of Wheeler's observations were carried forward—just at the period when the mature sexual forms were preparing to emerge from the nest. Numerous males were seen in many of these nests. In many of them callow females were also observed, but in a curious and anomalous condition. The nests were all located under large and rather moist eucalyptus logs, and in many of them superficial galleries were found to be crowded with *decidedly callow, yet dealate*, females. Often ten or fifteen individuals were seen in a single group, which fled precipitately into the lower galleries when pursued. Only one winged young female was found, and this was an exceedingly callow individual, the short wings of which barely reached the third gastric segment. On

the same day, a fully pigmented, solitary, isolated, colony-founding female of the same species was taken nearby under conditions exactly similar to those described by Wheeler, and a little further on an incipient colony, consisting of a queen and six young workers, was disclosed.

It seems likely that the larger colonies of *M. regularis* are normally pleometrotic, like those of *P. pilosula*, although it was not possible to prove this. It seems improbable in the extreme, however, that the crowds of dealate callow females found in the surface galleries of these nests were brood-queens which had returned to their parent formicaries after flight, for if this were true, emergence from the nest would have taken place while the queens were in a very callow and relatively helpless state. It seems much more probable to the authors, from these observations, that the young queens of *M. regularis* normally drop the wings while still callow and while still in the parental nest, thereafter, when mature, emerging wingless into the open to be fecundated on the ground or on bushes or trees and later to isolate themselves and begin new colonies in the fashion peculiar to these primitive ants. Such an assumption was later reinforced by the fact that six of these dealate callows, taken from four colonies, all isolated themselves after a period of wandering and excavated typical cells under artificial conditions, from which they foraged at intervals in normal fashion.

If this interpretation of the behavior of the young females of *M. regularis* be correct, it forms a natural transition to the situation in *Myrmecia tarsata*. Here the functional females are ergatoid in form, the thorax being workerlike, and the differences between the sexual females and the largest workers being but slight. The "nuptial flight" of this species was observed at length near Pymble, N. S. W., where the species is abundant, in March of 1948. Great numbers of winged males and wingless females were produced from numerous relatively large formicaries. The males promptly took flight and disappeared. The females wandered away slowly. Judging from these observations, and from confirmatory statements of Father John McAreavey (*in litteris*), these young females must wander for some time in the open, possibly for a period of several weeks, during which they are found and fertilized by the active males. Subsequently they form bivouacs and proceed to the establishment of the colony in the typical general pattern of the Myrmecii, as has been shown by McAreavey and as was confirmed in these studies with a number of young females taken wandering in the open.

The pattern of the nuptial flight among the Myrmecii is thus of a markedly primitive and generalized character, and is reminiscent of the mating procedure of many of the lower vespoids, solitary as well as social. Within this single tribe, there are elements corresponding to many diverging patterns among the more specialized ants, suggesting, though never quite attaining, the concerted, well-defined flights in such genera as *Atta* or *Lasius* on the one hand, in which the queens actively participate, and foreshadowing, but, again, never actually reaching the opposite extreme among the Dorylinae, on the other, in which the males, as Schneirla has shown (1948), apparently join the columns of the young females to fecundate them.

The method of colony foundation among the Myrmecii is likewise

extraordinarily primitive and generalized, and may well represent the ancestral mode among ants as a whole. It was first formulated extensively by Wheeler (1933) as a conjecture based upon a number of indirect observations. Clark (1925) had already recorded that the young females of a number of species of *Myrmecia* isolate themselves in single cells, sometimes alone and sometimes in company with others, and that young brood is present in such chambers, which is fed on insect prey supplied by the queen. Wheeler noticed further that such chambers were usually constructed with a superficial cell at the surface of the soil, which, while placed directly under a stone or log or other natural cover, was invariably located near the edge of the overlying object, so that it would be very easy for the imprisoned insect to remove a portion of the wall of the chamber and leave it periodically to forage. He found a few such cells containing active brood but no fertile female, and concluded that, at the moment of intrusion, the parent was absent. Confirmatory to this conjecture, he also succeeded in finding dealate females foraging in the open, as Clark had done before him.[2] These observations, together with that of a nest of *M. regularis* in which the soil at the margin of the brood-chamber had been freshly disturbed, led him to conclude with Clark that the young females of *Myrmecia*, following the nuptial flight, typically excavate and occupy a large brood chamber, which, though sealed to the outside, is so constructed that it can be opened, permitting the occupant to emerge to forage. He further concluded that this foraging is done quite regularly, both before and after the brood has appeared, and that subsequent to the hatching of the larvae, the female provides them continuously with insect food in addition to foraging for nectar to sustain herself. Wheeler was not able to confirm his conjecture by studies in the artificial nest. Clark (1934a) has done so, but has never published detailed accounts of the procedure. A re-investigation of the details of this significant process in the artificial nest therefore seemed worth while.

It has been a particular pleasure to be able to confirm the statements of Clark and of Wheeler by direct observation upon a number of species in the artificial nest, and to fill in the details of the entire process. Young females of *Promyrmecia piliventris*, *Myrmecia forficata*, *M. vindex*, and *M. regularis* observed under artificial conditions all constructed cells under stones, bits of logs, or darkened glass plates which closely resembled the natural ones described by Clark and Wheeler. The cells were carefully finished and closed to the outside when the owner retired into them. Wherever possible, such cells were provided with an upper chamber, directly at the surface and excavated near the edge of some covering support, and a lower one, two or three inches underground and connected by one or more short, wide, galleries. From the time that the cells were finished and closed (a process which for its rough completion required three or four days of more or less continuous work on the part of the female) they were opened regularly and the young queen issued to feed on the honey provided. Most of these feeding trips were nocturnal, and in some species, notably *M. regularis*, they took place with great regularity at about six o'clock each evening,

[2]Both of these observations were personally confirmed in the course of the present work: the first with *Myrmecia forficata* on Mt. Kosciusko, the second with *M. nigrocincta* at Pymble, N. S. W.

the female continuing to wander through much of the night but returning and closing the cell before morning. Within a few weeks the spherical eggs appeared, loosley scattered on the floor of the chamber, and were assiduously attended. Until they hatched, little attention was paid to insect food by the nurse, although it was occasionally licked. As soon as young larvae appeared, however, fragments of mealworms and other insect prey were regularly carried into the chamber on these nightly foraging expeditions and provided to the young. The larvae were kept in a compact packet and were licked avidly for exudates almost from the time of hatching, as earlier indicated. They developed relatively rapidly, and at maturity were banked with earth by the queen in typical fashion and the cocoons were exhumed and cleaned as soon as they were completed. At this time the female ceased to bring insect prey into the nest chamber, but continued to feed on it to a certain extent outside. The queen continued to forage until, and after, the young workers appeared.

A typical history of the foundation of a colony by a fertile female of *Myrmecia forficata* is shown below:

1947.	
August 15.	Young female established in artificial nest. Excavated typical chamber shortly thereafter and retired into it, emerging regularly at night to forage.
September 3.	Eight eggs found in nest.
September 29.	Group of small, newly-hatched larvae found feeding on mealworm fragment carried into nest by female.
October 4.	Four larvae, apparently about one-quarter grown, observed in nest.
October 28.	One small but perfect cocoon and two apparently half-grown larvae observed.
October 29.	One cocoon, one larva, and one larva banked with earth and in the process of spinning.
October 31.	Three cocoons in nest.
November 3.	Three cocoons, closely guarded by female.
November 8.	Three cocoons, which have been removed to the driest portion of the chamber excavated by the queen, and are closely guarded.
December 12.	First cocoon eclosed small but perfect young worker.
December 16.	Second cocoon eclosed small but perfect young worker. The third cocoon failed of eclosure.

This whole primitive and generalized picture of the initiation of the social structure among the Myrmecii is of the highest significance for our understanding of the basis of formicid society in general, and is deserving of more quantitative study than it has so far received. It will be important to know, for instance, whether the degeneration of wing-musculature in the female with the consequent increment of nutritive material, which is initiated at dealation among many if not most of the higher forms, is duplicated among the Myrmecii. Studies of the histology of the wing-musculature in such queens among the Myrmecii and the Amblyoponii are in progress at present. Preliminary results indicate that quite probably no such coordinated breakdown takes place in these primitive forms, and that the wing muscles therefore may not constitute any sort of food reserve, as they do among higher ants.

If this situation should be more completely confirmed, it will be interesting to notice that it is precisely among those forms in which wing-muscle degeneration does not occur and where foraging of the colony-founding queen is the rule that wingless worker-like females with reduced thoraces occur so frequently, a conclusion which may suggest that the primary evolutionary significance of bulky wing-muscles in the higher ants is as a tissue reservoir, and that the specialized flights which they make possible may be of secondary significance in evolutionary terms, representing a desirable, but by no means an essential, means of securing the dispersion and the genetic heterozygosity evidently important to the survival of the species. This question is being investigated much further.

Among those higher ants in which the young females form their colonies in typical solitary and claustral fashion, the maturing of the first brood of workers coincides fairly closely with a significant change in the behavior of the queen. The general nest-functions which she has hitherto served are almost entirely abandoned, her activities are restricted very largely to egg-laying, and she becomes wholly dependent upon the workers for food. This change does not occur, or occurs very gradually, in *Myrmecia*. When the first brood of workers is mature, the fertile female continues to forage with them outside of the nest for some time, at least in *Myrmecia gulosa*, *M. forficata*, and *M. regularis*, where such behavior has been often observed. This pattern is in fact essential for the queen, since the workers are unable to distribute ingluvial food to her. Throughout the rearing of the second and more numerous group of larvae, therefore, the queen probably continues to be the most significant single factor in all phases of colonial activity.

The subsequent picture is much less clear, and presents a fascinating problem. Does the queen continue to emerge from the nest to forage throughout the life of the colony? In the artificial nest, mature, and indeed very old queens of *Promyrmecia pilosula* and *P. piliventris* in relatively populous colonies regularly continued to emerge with the workers to feed at the honey dishes. When removed from populous colonies, or when deprived of most of their worker personnel, old females of *Myrmecia tarsata*, *M. forficata*, and *M. vindex* have in the artificial nest reverted almost immediately to the behavior pattern of young colony-founding females, emerging regularly to forage and assiduously tending larvae entrusted to them. In several instances these females were taken from very large colonies and since, in these species, the colonies regularly contain only the founding females, they must have been several years old at the time of capture. Such a ready reversion to independent existence, even at an advanced age, emphasizes once again how lowly specialized the perfect female of *Myrmecia* and *Promyrmecia* is to a social structure.

It is questionable whether this regular emergence of the old female to forage which has been repeatedly observed in the artificial nest occurs in the wild, and it has not yet been possible to establish this through field observations. Fertile brood females in large colonies of all the species examined were always found—when they could be taken at all—in the lowest and most remote reaches of the nest, and were in general full-fed and somewhat physogastric, suggesting that some

source of nourishment was available within the formicary. It is very conceivable that the fertile female, to an even greater extent than the smallest workers, may subsist on larval exudates and on insect food brought within the nest during the height of the brood-rearing season. What the behavior of such females may be at other times, however, remains a puzzle to be elucidated.

It follows from what has been said that the social position of the queen of *Myrmecia* or *Promyrmecia* within the colony is little different from that of a worker. As among so many of the lower Ponerinae, no special attention is paid her, and except for the fact that she is somewhat more sedentary, somewhat more highly fertile, and somewhat less aggressive than the workers, there is little behaviorally to differentiate her from the rest of the colony personnel.

FERTILITY OF WORKERS, AND DEVELOPMENT OF WORKER-LAID BROOD

In all the species of *Myrmecia* and *Promyrmecia* observed in the artificial nest, the workers have been highly fertile and have contributed markedly to the brood of the colony. Worker-laid eggs have been reared to maturity in colonies of *Promyrmecia piliventris* and *Myrmecia nigrocincta* in which fertile females were not present. In every case, such broods consisted entirely of males, thus agreeing with the usual situation reported among the higher ants, although this does not appear to be invariable (Haskins and Enzmann, 1945).[3]

SENSES

The Myrmecii are very unusual among ants in that vision is predominantly relied upon as a factor in orientation outside the nest during daylight hours. The large. convex compound eyes are exceedingly sensitive in detecting movement, and every action of the insects in foraging is indicative of the reliance placed in them. Among many species of *Myrmecia*, the antenna are never brought into play during daylight foraging except in actual exploration for prey. As previously observed, no evidence of the trail-following procedures so characteristic of higher ants could be found during daylight in the two-day series of observations of *Myrmecia gulosa* recorded. After dark, however, and presumably underground, the situation is very different. Observation of some ten colonies of *Myrmecia gulosa* were made during the night of January 13, 1947 (when the daylight observations recorded had just been completed). The night was very dark, and observations were made with the aid of a dim taper. They disclosed undiminished activity on the nest crater, but of a very different kind from that of the daylight hours. There was no foraging, and activity was restricted to excavation. Streams of ants were passing to and fro on the crater, building up its rim with earth granules. On these trips, which were limited in scope to two or three feet, the antennae were brought into play constantly, and there was no evidence of any reliance upon vision. The ants were wholly insensitive to the light of the taper even when brought close to them, and displayed no reaction whatever to gross movements in their immediate vicinity. No contrast could have been

[3]Brood brought to the late pupal stage by two artificially dealated infertile females of *Promyrmecia piliventris* was likewise male.

greater to their highly observant, sensitive, and aggressive attitude during the daylight hours.

Two series of experiments were made in an attempt to determine the ability of the Myrmecii to distinguish colors, and the significance of color vision for them. Both were negative. In the first, colored plastic cups were used in the experiments described with *M. gulosa* and the colors were interchanged about the nest at intervals. No indication was ever found that a marked worker, having become habituated to visiting a cup of a particular color, tended to follow that color when it was interchanged with another. Instead, position seemed to be the governing factor, and any new color that was substituted was accepted readily. If both colors were moved to new positions, the individual wandered at random until one or the other was discovered, and thereafter returned to that spot. In these experiments at least, therefore, color appeared to have no significance.

In the second series, several pairs of Wratten filters, so chosen as to transmit equal intensities of light in widely separated portions of the spectrum, were placed over glass Lubbock nests containing colonies of *Myrmecia nigrocincta* and *M. tarsata*. These nests, normally kept in darkness, were then strongly illuminated with white light. Brood was carried under the filter squares, as was expected, but an interchanging of the squares was not followed by any shift in the quantities of brood under each, nor in any tendency of one ant to follow a particular square. This behavior is in rather marked contrast to the normal behavior of many higher ants which have been tested under similar conditions, in which the filters transmitting longer wave lengths are almost invariably preferred. It is also unlike that of *Euponera gilva* in experiments earlier reported (Haskins, 1931), in which individuals tended to follow a given filter. It has so far proved impossible to determine whether there are marked differences in sensitivity of light perception in different portions of the spectrum in *Myrmecia* and *Promyrmecia*.

Experiments to determine the existence of a sense of hearing in *Myrmecia* and *Promyrmecia* proved almost as difficult and unsatisfactory as those connected with vision. The primary difficulty was the detection of a visible reaction to sound, since the insects, although very alert and reactive, are inclined when startled to "freeze" to immobility, and thereafter to exhibit no further responses to stimuli. It was, however, possible to demonstrate reactivity to musical notes covering the chromatic scale (Table I), although such reactions, while positive, were sporadic. Lubbock nests containing colonies of various species were mounted on multiple layers of turkish toweling, resting in turn on an upholstered support, to eliminate mechanically transmitted vibration in so far as possible, and notes were sounded with a pitch pipe some three inches above the covering glass of the Lubbock nest. The nests were so arranged that the ants were fully protected from air currents. Each note was sounded three times. Five trials of the chromatic series were made for each nest, each trial being separated by a resting period of from fifteen to thirty minutes, each series being recorded separately. Each series for the same nest was begun alternately at the high and the low end of the scale. The method used was that described by Haskins and Enzmann (1938) in tests with various other ants. The

TABLE I

REACTION OF VARIOUS SPECIES OF MYRMECIA AND PROMYRMECIA TO NOTES OF THE CHROMATIC SCALE

SPECIES TESTED	F		F#		G		G#		A		A#		B		C		C#		D		D#		E		F	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
Myrmecia forficata (1)	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5
Myrmecia forficata (2)	4	1	2	3	2	3	1	4	0	5	0	5	0	5	2	3	1	4	1	4	3	2	2	3	3	2
Myrmecia vindex (1)	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	2	3
Myrmecia vindex (2)	1	4	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	0	5	1	4	0	5	2	3
Myrmecia tarsata (1)	1	4	1	4	2	3	0	5	1	4	1	4	0	5	1	4	2	3	2	3	4	1	3	2	3	2
Myrmecia tarsata (2)	3	2	0	5	1	4	1	4	3	2	0	5	3	2	1	4	1	4	4	1	4	1	3	2	4	1
Myrmecia nigrocincta	1	4	2	3	3	2	3	2	1	4	2	3	2	3	1	4	1	4	1	4	2	3	4	1	3	2
Myrmecia swalei	1	4	3	2	1	4	2	3	1	4	3	2	4	1	4	1	5	0	4	1	4	1	5	0	4	1
Promyrmecia piliventris (1)	2	3	2	3	0	5	0	5	0	5	0	5	0	5	0	5	0	5	1	4	1	4	2	3	4	1
Promyrmecia piliventris (2)	2	3	3	2	3	2	1	4	1	4	1	4	3	2	3	2	3	2	4	1	3	2	4	1	4	1
Promyrmecia piliventris (3)	1	4	2	3	2	3	2	3	1	4	1	4	2	3	3	2	3	2	2	3	3	2	3	2	2	3
Promyrmecia piliventris (4)	2	3	1	4	1	4	1	4	0	5	0	5	1	4	0	5	1	4	0	5	0	5	2	3	2	3
Promyrmecia pilosula (1)	2	3	3	2	2	3	2	3	2	3	0	5	1	4	4	1	1	4	2	3	4	1	3	2	2	3
Promyrmecia pilosula (2)	2	3	3	2	1	4	1	4	0	5	0	5	0	5	1	4	0	5	3	2	2	3	1	4	2	3
Promyrmecia pilosula (3)	1	4	2	3	1	4	1	4	2	3	1	4	4	1	3	2	3	2	4	1	3	2	3	2	3	2

+ = positive observations.
− = negative.

results were as shown. It will be seen that some positive reactions were secured for most of the species over the entire chromatic scale.

The olfactory sense, though less constantly used than among most of the higher ants, is nevertheless acute, and is evidently employed extensively in the location of food and within the nest. Its keenness is well attested by the ease with which alien ants, even of the same species, are detected in the colony, as already described. It is also well shown by the violence of reaction to various foreign odors about the nest region, even when these are in rather extreme dilution. As in the higher ants, there seems much evidence that the olfactory sense is closely associated with the tactile sensory areas of the antennae. It seems probable that the two classes of sensations are very considerably fused.

Taste is also highly developed, as among the higher ants. The Myrmecii are discriminating in their choice of nectarivorous substances. Small quantities of strong-tasting foreign matter included in solution with honey will result in its immediate rejection.

SIZE OF COLONIES

The loose structure and the low degree of co-ordination so characteristic of the Myrmecii would lead the observer to expect that such colonies would, on the whole, be quite limited in numbers. It has been generally supposed that the colonies of *Myrmecia* and *Promyrmecia* rarely exceed 200 individuals. This is true of some forms, and colonies of such size are not uncommon in most. There are, however, certain striking exceptions, notably in such species as *Myrmecia regularis*, *M. tarsata*, *M. gulosa*, *Promyrmecia piliventris*, and *P. pilosula*. To determine this question more accurately, a number of colonies of several species were extracted as nearly completely as possible and the members counted. These counts were made at approximately the height of the season of growth, after the greater portion of the worker and sexual brood had been eclosed, and just before or just after the sexual forms had left the parental nests. The results of these counts were as shown in Table II.

Attention may particularly be drawn to the second colonies of *Promyrmecia pilosula* and of *Myrmecia gulosa* listed above, for which the counts exceeded 1000 and 2000 individuals respectively. Both of these colonies were in situations which were difficult to excavate, and, despite some eight hours of work with each of them, it was never possible to penetrate to the center nor to discover the brood queens. It may be conservatively estimated that not more than 70–90% of the individuals in these colonies were counted. These colonies, moreover, were not especially remarkable for their size.

It is interesting to reflect, therefore, that several species of *Myrmecia* and *Promyrmecia* probably are able to maintain larger stable communities than a very considerable proportion of the higher ants, despite the generalization of the workers, the relatively low fertility of the queens, and, above all, the absence of the habit of distribution of ingluvial food among the workers. This last bond of colonial solidarity seems so basic among the higher ants that it is most surprising to see it successfully substituted in the Myrmecii by other influences. Chief among these, undoubtedly, are the strong individual fixations of the

workers for the nest locality, and the focal stimuli provided by a plentiful supply of brood during the season of maximum foraging. The importance of the brood as a social stimulus is well illustrated by the extreme precision of co-ordination between the foraging habits of the workers and the state of development of the brood already mentioned. A further stimulus, of a negative kind, may be offered by the extreme

TABLE II

COUNTED NUMBERS IN COLONIES OF MYRMECIA AND PROMYRMECIA

Species	Location	Date of Count	No. of Individuals
Myrmecia vindex	Perth, W. A.	Mar. 15, 1948.	1 mature female 12 winged females 94 workers 12 pupae Total: 119
*Myrmecia vindex**	Bellevue, W. A.	Mar. 3, 1948.	4 winged females 268 workers 10 pupae 10 larvae Total: 292
*Myrmecia gulosa**	National Park, N. S. W.	Mar. 22, 1948.	188 workers 23 cocoons Total: 211
*Myrmecia gulosa**	Sutherland, N. S. W.	Mar. 24, 1948.	1586 workers 424 cocoons 104 larvae Total: 2114
Promyrmecia pilosula	Ferntree Gully, Victoria	Feb. 26, 1948.	4 mature females 549 workers 178 pupae Total: 731
*Promyrmecia pilosula**	Ferntree Gully, Victoria	Feb. 26, 1948.	55 males 807 workers 206 pupae Total: 1068

*In these cases, it was impossible, in the time available, to extract the complete colony. It may be guessed that the numbers given represent 70–90% of the entire personnel.

hostility of alien colonies to workers that may attempt to seek refuge in them. It may well also be that stability of colonial organization is promoted by an unusual natural life span of both fertile female and worker. This question is under present investigation.

PARASITES AND COLONIAL SYMBIONTS

The simplicity of colonial organization in the Myrmecii, their vigilance, and their implacable hostility to such alien intruders as they

detect within their formicaries result in a paucity of parasites or colonial symbionts unusual among such large ants harboring such an abundance of potential food material within their formicaries. The most conspicuous true parasites commonly found in the nests are undoubtedly the chalcidids of the genus *Eucharis*, several species of which are frequently associated with various species of *Myrmecia* and *Promyrmecia*. They attack the larvae exclusively. Wheeler (1933) has shown that adults of *Myrmecia* are sometimes infested with the parasitic nematode *Mermis*. No such individuals were encountered in the present studies.

Few smaller ants are to be found in the immediate vicinity of the nests of *Myrmecia* and *Promyrmecia*, for the vigilance of the large ponerines makes invasion or theft by the alien species difficult. An exception is provided, however, by the specialized ponerine *Brachyponera lutea*, one of the commonest and most ubiquitous ants of Australia, unique among ponerines in the remarkable differentiation, both in size and form, between its queens and workers. This species, which tends to nest close to the formicaries of many ants and colonies of termites, is quite capable of securing the eggs and young larvae of *Myrmecia* without being detected, and is not infrequently found nesting in or near the craters of such larger species as *Myrmecia gulosa*.

Perhaps the most interesting relation with alien species to be found among the Myrmecii, however, is that existing between *Myrmecia regularis* and the small toad *Pseudophryne nicholsi* Harrison, a relation first reported by Barbour and Loveridge (1929) at Manjimup, in southwestern West Australia. The toads were found again in this locality by Wheeler and Schevill (Wheeler, 1933). It was possible in the course of the present work to fully confirm the findings of Barbour and Loveridge at Manjimup, and also to study the toads in the artificial nest in association with their normal host, and with other species of *Myrmecia* and *Promyrmecia*.

The toads, small and rather fragile, rarely exceed 25 mm. in length, are of a plain dark-brown coloration, and normally live subterranean lives concealed under heavy rocks or logs in the normally rather damp soil of the region. Here they crawl about slowly in search of insect prey. They have never been seen to hop, even when opportunity was provided to do so. They are unusual among the anurans in that the eggs, laid in the soil, hatch directly into small perfect toads, the tadpole stage having been completed in the ovum.

Numerous specimens of *Pseudophryne* were seen and captured at Manjumup during March, 1948. All of them were located in the central galleries and chambers of large and pugnacious colonies of *M. regularis*, which swarmed over them when the nests were disturbed, but which, even when most excited, paid no attention to them whatever. Captured specimens of *Pseudophryne* were introduced into colonies of *M. regularis* housed in Lubbock nests, where they lived successfully for several months. Neither ants nor toads paid the slightest attention to one another, notwithstanding the fact that the toads wandered throughout the ants' nests, and examined the brood piles—a procedure which would not have been tolerated from any other intruder. The toads were never seen to attack adult ants or to menace the brood. Instead, they fed by "lapping" podurans and similar small insects

which collected in the vicinity of the rather massive underground kitchen middens maintained by the *Myrmecias*. The toads were always most abundant in the vicinity of these piles of discarded insect fragments, and it seems probable that much if not all of their normal subsistence was obtained in this manner.

An individual *Pseudophryne* was transferred from its colony of *M. regularis* to a colony of *P. pilosula*, and the reactions observed. Interestingly, they were not immediately overtly hostile on the part of the ants, but it was evident that the presence of the toad was definitely detected by *Promyrmecia* and it was eventually attacked.

The relationship with *M. regularis* is evidently specific, but it is almost certainly facultative. Many colonies of *M. regularis* were found without the toads, and, although the toads were not found separate from the ants in the course of these studies, made in March, Wheeler and Schevill, collecting in November, found only specimens that were living apart from the ants. It seems probable that the toads are attracted into the ant colonies later in the season, when the refuse collected in the kitchen middens has become more abundant, and when these have therefore become focal points for the minute insects on which it is to be presumed that *Pseudophryne* normally subsists.

ACKNOWLEDGMENTS

We should like particularly to extend our very great thanks to Mr. and Mrs. Frank Nicholls and Mr. John Clark of Melbourne for their assistance in many phases of this study. Through their kindness in sending living material from Australia it was possible to undertake studies in the artificial nest several years before material could be personally observed in the field. Mr. Clark was likewise so kind as to furnish an extensive collection of preserved material which was of the utmost help in gaining familiarity with the structural features of the group. Finally, his advice and assistance, both through letters and personally after our arrival in Australia, were invaluable.

Thanks are also due to his student, Father John McAreavey, S. J., now of Canisius College, Pymble, N. S. W., for most kindly sending living material of *Myrmecia tarsata*, *M. gulosa*, and *M. nigrocincta*, as well as much information. We are particularly grateful to Dr. T. C. Schneirla, of the American Museum of Natural History, for much assistance and advice, and to him, Dr. F. S. Cooper, and to Miss Sarah Lichtenberg for most valuable help in maintaining observations on and carrying forward colonies in the artificial nest during the period of the Australian studies.

Our gratitude is also expressed to Dr. J. Bequaert of the Museum of Comparative Zoology of Harvard University, and to Dr. Herbert F. Schwarz of the American Museum of Natural History, for most kindly making it possible for us to study extensively the collections of *Myrmecia* and *Promyrmecia* in those institutions.

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PHYLLODY OF CHRYSANTHEMUM AND THE ERIOPHYID MITE, PARAPHYTOPTUS CHRYSANTHEMI KEIFER[1]

E. P. BREAKEY[2] AND G. S. BATCHELOR[3]

On October 19, 1948, a florist of Woodinville, Washington, brought some chrysanthemum plants that were dwarfed and stunted to the Western Washington Experiment Station. The older leaves on these plants were distinctly reddish in color and no flowers had formed on some of them, while others bore a few that were severely deformed. Careful examination of the plants disclosed that the flower parts had

FIGURE 1

FIGURE 2

FIG. 1. Phyllody of the chrysanthemum involving altered and stunted growth. Note phylloid flowers in axils of leaves.

FIG. 2. Phyllody of the chrysanthemum. Leaves have been removed to show shortened internodes.

become vegetative and that their formation had been altered early in their development. Also, the stems were shortened between the

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internodes (fig. 2), and there was an increase and a clustering of the stems resulting in a witches'-broom effect (fig. 1). Numerous eriophyid mites, *Paraphytoptus chrysanthemi* Keifer (fig. 3), were found in these deformed "buds." The presence of these mites and the fact that related species of mites are known to cause malformations of various kinds in other plants suggests that they are the probable cause of the "disease" of the Woodinville chrysanthemums.

Heald (1) defines phyllody as follows: "The term 'phyllody' is applied to the change of floral organs into leafy structures. While phyllody is frequently caused by the presence of a parasite, other disturbances may produce similar effects." More recently, Dana (2) defined phyllody as "A vegetative change in the flower by which some or all of the parts of the flower become more or less leaflike." It was interesting to note that some of the phylloid flowers of the chrysanthemums bore traces of the coloring that would normally have been depos-

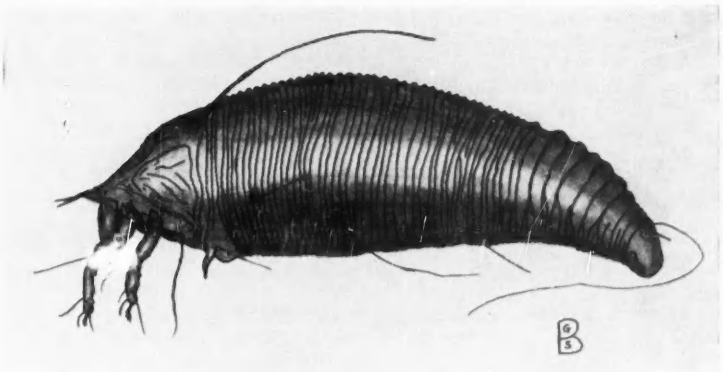

FIG. 3. The eriophyid mite, *Paraphytoptus chrysanthemi* Keifer.

ited in the flowers. It seems that the chrysanthemums in question fulfill all the requirements of the definitions, and that we are concerned with a case of true phyllody.

The family Eriophyidae contains rust mites, blister mites, erinose mites, gall mites, bud mites, and the blackberry mite, *Eriophyes essigi* Hassan, cause of the red berry disease of the blackberry. Smith and Stafford (3) found that the bud mite of grapes, *Eriophyes vitis* (Pgst.), caused a pronounced shortening of the internodes of new growth in the spring, flattened canes, and killed the terminal buds. The killing of the terminal buds resulted in the development of a witches'-broom growth of new shoots and in the production of zigzagged shoots. Many years ago, Kerner and Oliver (4) described a fasciation of the ash, *Fraxinus excelsior* L. and *F. ornus* L., which was caused by a mite of the genus *Phytoptus* (*Eriophyes*). The similarities between the ways in which the bud mite affected the development of the grapes and *Para-*

phytoptus chrysanthemi altered the development of the chrysanthemums are apparent.

Keifer (5) originally found *Paraphytoptus chrysanthemi* around the leaf-axil buds and in the terminal flowers of the chrysanthemums from which he obtained the type sepcimens. He commented, however, that no damage was noted. It is possible, of course, for mites belonging to this group to be present on the plants and produce no evident damage. However, in the instance being reported, damage was great and accounted for practically 100 percent loss in flowers. The three varieties of chrysanthemums observed by the writers as being affected by the presence of these mites were *Wendy*, an early English bronze, *Red Rover* and *Lavender Lady*. All varieties were grown out-of-doors for cut flowers.

In discussing the situation with the florist, particularly with reference to the origin of the infestation, it was suggested that it may have originated with a shipment of chrysanthemum varieties that were obtained from Japan soon after the close of the recent war. First indications of the condition appeared in 1947, but were not pronounced and were not given serious consideration.

A review of the literature indicates that we are apparently reporting the first probable relationship between phyllody and eriophyid mites.

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This volume, which concludes the Lepidoptera (see review of Part 1, Ann. Ent. Soc. Amer. 39:241, 1946), covers the Macrofrenatae, or, more specifically, the superfamilies Pyralidoidea, Drepanoidea, Sphingoidea, Geometroidea, Uranioidea, Notontoidea, Noctuoidea, Mimallonoidea, Saturnioidea, Bombycoidea, Lasiocampoidea, Hesperioidea, Papilionoidea, and Nymphaloidea. The plan and quality of the work is comparable to that of the preceding part.

As would be expected, considerable space is devoted to the economically more important insects; for example, sixteen pages are given to the sugar cane borer, *Diatraea saccharalis* (F.). Some pests common to North American and Brazil, for example, *Galleria mellonella* (L.), *Plodia interpunctella* (Hübner), *Heliothis obsoleta* (F.), and *Alabama argillacea* (Hübner), are treated in like fashion, and the inclusion of some non-Brazilian pests, such as the European corn borer, is something of a surprise. Among the more interesting material included is a discussion of moths ectoparasitic in the fur of living sloths (p. 25). Also deserving of mention are the descriptions of the migratory habits of *Urania* (pp. 146–7) and of the aquatic habits of the larvae of the arctiid *Pallustra* (pp. 227–9).—M. T. J.

ENTOMOGENOUS FUNGI OF THE GENUS METARRHIZIUM ON WIREWORMS IN THE PACIFIC NORTHWEST

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During 1932 to 1942 facilities for the culture and study of entomogenous fungi were available at the Forest Grove, Ore., station of the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture. The writer devoted some time to this work, especially in the winter months, and the following information on two species of *Metarrhizium* was acquired at that time.

Metarrhizium brunneum Petch

This species was described by Petch in 1935 (5) from material "on a homopterous insect (Cicadellidae), collected at Laguna, Philippine Islands, December, 1931." On June 25, 1933, T. R. Chamberlin discovered a fungous outcropping on four larvae of *Limonius* sp. being reared in their native soil in tin salve boxes at Forest Grove. Mr. Chamberlin had collected these wireworms in a field on Gales Creek bottom land about 5 miles northwest of Forest Grove. The soil in this area is classed as Chehalis Silt Loam (Watson *et al*, 9). By July 7 all four wireworms had died of a fungous disease. A pure growth of fungus had developed in all. A white cottony mycelium appeared first, some of which spread out in interwoven, Isaria-like strands for as much as 20 mm. beyond the body of the insect. On the ends of these strands, palisade-like layers of spores were formed. The color of this sporiferous layer was light drab (Ridgway, 6), blending with the color of the soil. The spores clung together both laterally and linearly and the spore masses broke up, when touched, into sharp angled, columnar aggregations resembling talus. The normal cylindrical spores were measured, with an ocular micrometer, as 7.4 to 9.2 microns by 2.5 to 2.8 microns. Some smaller spores measured 5.5 by 1.8 microns. These measurements come within the limits of *Metarrhizium anisopliae* (Metsch.), but the color was quite different, and the writer concluded that the fungus was an undescribed species of *Metarrhizium*.

Transfers were easily made direct from the wireworms to potato, on which the fungus overgrew any secondary infection by bacteria or fungi. It was later grown in pure culture on several media, including meat, fish, and custard. On potato the color of the sporiferous layer was somewhat darker—wood brown or drab (Ridgway, 6)—than on the wireworms, but the spore measurements remained constant. In cultures the mycelial layer was white, with a narrow, cinnamon-brown

[1]Retired October 31, 1948.

(Ridgway, 6) streak next to the substratum, closely woven, tough and mat-like. The drab sporiferous layer on flat cultures in Erlenmeyer flasks had a slightly roughened or pebbled surface, not as smooth as that of *M. anisopliae*. This pebbled surface appeared to be caused by differences in the length of the branches of the sporophores at the time of spore formation. In *M. anisopliae*, all branches appear to reach the same level, like a corymb, before producing spores. Cultures of *M. brunneum* sometimes formed round-headed bodies after the brown sporiferous layer had been formed, when outcrops of the snowy-white mycelial layer pushed through. Some of these puffball-like bodies never seemed to develop spores on their periphery, and a culture taken from this extruded mycelium made a sparse growth and remained sterile. It was noted that, in culture, *M. brunneum* produced a longer mycelial growth and began spore production about 5 days later than did *M. anisopliae*.

Dr. Vera K. Charles of the Bureau of Plant Industry, Soils, and Agricultural Engineering, United States Department of Agriculture, suggested, in a letter dated April 2, 1936, that this fungus might be "*M. brunneum* of Petch, but your spores exceed the measurements given for this species." On September 27, 1943, cultures of this fungus were sent to the Northern Regional Research Laboratory, Peoria, Illinois, where the fungus was given the designation "*Metarrhizium* sp. NRRL 1944, Rockwood No. 1." Dr. W. Lawrence White, of the Farlow Reference Library and Herbarium of Cryptogamic Botany, Harvard University, has since written (letter of June 10, 1948) that he had worked some with this fungus, which he had obtained from Dr. Raper of the Northern Regional Research Laboratory. He stated that Dr. Petch had confirmed his identification of the fungus as *M. brunneum* Petch. In 1940 several large cultures of this fungus (in milk bottles) were sent to F. H. Shirck, of the Bureau of Entomology and Plant Quarantine, at Parma, Idaho. On June 18, 1940, spores from these cultures were mixed with soil and placed with several thousand wireworms in moist soil. The wireworms were later released in six locations near Parma.[2]

Metarrhizium anisopliae (Metsch.) Sorokin

This entomogenous fungus has been known since 1879 and has been recorded on various insects and under several names. Among these names are *Entomophthora anisopliae* Metsch. (Metschnikoff, 1879), *Oospora destructor* Delacroix (Delacroix, 2), and *Penicillium anisopliae* Vuillemin (Vuillemin, 8). Petch (4) has reviewed the genus and discussed variations in the size of the spores.

The writer was familiar with this fungus, as he saw many specimens from several localities, mostly on elaterid larvae, but also on tenebrionid larvae, on scarabaeid larvae, pupae, and adults, on noctuid larvae and pupae, and on *Sphenophorus* larvae. In 1914 he infected adults of *Hypera postica* (Gyll.) with this fungus in the laboratory and found it less virulent to weevils than *Beauveria globulifera* Speg. (Rockwood, 7). At that time he observed fungous bodies in infected but still living

[2]Personal correspondence with F. H. Shirck, February 16, 1942.

weevils. Some of these bodies, in silkworms, have been illustrated by Glaser (3).

In 1925 Barss and Stearns (1) recorded this species on the European earwig, *Forficula auricularia* L., and other insects in Oregon. The writer saw this fungus in the Pacific Northwest on an *Omus* larva collected near Forest Grove by Sadie E. Keen on August 4, 1922 (spores 4.6 to 8.3 microns by 1.9 to 2.9 microns); on *Euxoa atomaris* Smith larvae collected on March 26, 1926 near Forest Grove (spores typical); on *Porosagrotis vetusta* (Walker) larvae, and parasite *Amblyteles*, collected near The Dalles, Oregon, on April 25, 1928 (spores 3.7 to 6.6 microns by 2.8 microns); on *Agrotis ypsilon* (Rott.) larvae collected near Gaston, Oregon, on July 31, 1938 (spores 6 to 8 microns by 3 microns); and on the carabid larva, *Amara obesa* Say, from Klamath Marsh in northern Klamath County, Oregon, on May 23, 1936 (spores typical). The fungus was obtained in pure culture from this last specimen and is hereafter called the Amara strain. The color of the sporiferous layer of this strain was between deep grayish olive and Andover green (Ridgway, 6).

In 1937 a strain of *M. anisopliae* on a wireworm *Limonius californicus* (Mann.), collected near Parma, Idaho, by Mr. Shirck, was brought into pure culture with considerable difficulty because the natural material was contaminated by bacteria and saprophytic fungi. This strain is hereafter referred to as the Idaho strain. The sporiferous layer of this fungus has a somewhat paler green color—Lincoln green (Ridgway, 6)—than that of the Amara strain, although the spores measure the same, 7 microns by 2.5 to 2.75 microns. Cultures of this strain were also sent to the Northern Regional Research Laboratory on September 27, 1943. On wireworms this fungus showed a short mycelial growth externally, forming cushion-like outcroppings at the sutures.

INFECTION EXPERIMENTS

The writer was supplied by Mr. Shirck with large stocks of wireworms for experimental purposes during 1936 to 1941. Naturally infected wireworms, a very small percentage in these stocks, were eliminated by holding them for a month or more in the original containers and culling dead worms before infection experiments were conducted in tin salve boxes containing sterilized Gales Creek sand. The most disturbing factor in these experiments was not prior infection with fungus, but the presence of mites on the wireworms. In one year, when the wireworms had been kept overlong at room temperatures, mites caused a large loss of wireworms. Infection by the fungi was brought about in two ways, by shaking the wireworms in a container with the dry spores before the wireworms were introduced into sterilized cans containing moist sand, and by introducing into sterilized cans containing moist sand a small amount of sterilized dry sand mixed with a measured quantity of spores and then putting the worms in the cans. The two methods were about equally effective in securing infection. Check lots of wireworms were kept in cans of moist sand, which had not been inoculated. In one series with *M. anispoliae* Idaho strain six times the usual amount of inoculum increased the mortality of the

wireworms to 57% compared with 32% in the cages receiving the usual amount of inoculum.

It was soon noted that in different cages of the same series there was a wide variation in the time required for the wireworms to become infected, and that the wireworms showed infection soon after molting. Apparently the wireworms were susceptible to infection only at the time of ecdysis. Infection and mortality consequently were prolonged over a period of several months after the inoculation of the sand in the cages.

The spores of all species or strains of *Metarrhizium* were dead in old cultures after 18 months.

These infection experiments showed that the Amara strain of *M. anisopliae* had little or no virulence for wireworms. In comparative infection experiments *M. brunneum* showed greater virulence for wireworms than did the Idaho strain of *M. anisopliae*. Although *M. brunneum* had been in artificial culture for 7 years before these experiments were concluded, it showed no impairment of virulence.

The comparative experiments, which were carried on in parallel series from 1937 through 1941, can be summarized as follows: *M. anisopliae* (Idaho strain), 15 series, mean percentage of mortality from fungous infection, $49.5\% \pm 3.9\%$; *M. brunneum*, 12 series, mean percentage of mortality from fungous infection, $72\% \pm 4.6\%$.

These experiments bring out the differences in virulence to wireworms among different species or strains of fungi of the genus *Metarrhizium*, and suggest that it might be worth while to look for strains of entomogenous fungi that are especially virulent to different species of insects. The hyphomycetous fungi have the advantage over the Entomophthoraceae, in that they are easily cultured and their virulence to insects is not impaired by artificial culture over long periods.

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NESTING ACTIVITIES OF TRACHYMYRMEX FOREL (HYMENOPTERA: FORMICIDAE) IN EAST TENNESSEE[1]

A. C. COLE

The genus *Trachymyrmex* is thus far represented from Tennessee by a single form, *T. septentrionalis seminole* Wheeler, one of seven species and subspecies known from the United States. Dennis (1938) records this variety as being very commonly represented in the Mississippi Embayment region of western Tennessee, the only part of the state from which he collected it. The following statements are quoted from the paper by Dennis: "The valley is protected on the north and west by mountains and the temperature is higher than in locations without this protection from the west and northwest storms. This fact probably explains the presence of these species[2] in East Tennessee." C. H. Kennedy took the species in the bottom land of Townsend Valley, east of the Chilhowee Range of eastern Tennessee (Dennis, 1938). The writer found nests of *seminole* in Wears Cove, Great Smoky Mountains National Park, in an open, dry, sandy area comparable to that in which colonies were located by Kennedy.

One might expect colonies of *seminole* to exist in the types of places already mentioned and indeed even at Knoxville, Tennessee, where the writer has noted two nests. However near the very top of Dupont Mountain—a part of the Chilhowee Range having an elevation of 3,600 feet—the writer discovered in July and August, 1949, two flourishing colonies of *seminole*. Temperatures at that elevation are such that the discovery came as a matter of considerable surprise.

At 10:30 A. M., on July 31, 1949, two *seminole* workers were observed on the crest of a rocky north-facing bluff while they were carrying bits of green leaves in their mandibles. The workers were followed to their nest which was located in moist and rather sandy soil beneath the edge of a rocky ledge and was accessible only through a single narrow gallery marked by an inconspicuous, circular, unshaded entrance approximately 0.5 cm. in diameter. The nest contained a fungus garden, with a volume of approximately 23.75 cc., pendent from a root which traversed the length of the single nest chamber. The chamber was situated at a soil depth of 12.5 cm., and it was connected to the nest entrance by a gallery 15.5 cm. in length. The entire nest contents were collected and subsequently examined. The nest site was observed carefully for foraging workers returning to the nest. A total of fourteen ants returned during approximately the first two hours of observation, and inasmuch as no additional ants made an appearance within an additional hour, the writer believes that the entire numerical strength

[1]Contribution No. 30, Department of Zoology and Entomology, The University of Tennessee, Knoxville.

[2]Dennis includes *Dorymyrmex pyramicus flavus* McCook.

of the colony was represented in the bulk collection. Counts showed a total of 284 workers, 29 alate females, 8 dealate females, 19 larvae, and 67 pupae (chiefly those of workers). No males were in the colony at the time of observation and no male pupae were found. Although eggs were not located, they were undoubtedly in the interstices of the fungus mass and were obscured by the mycelia.

On August 10, 1949, removal of a large imbedded rock from the sandy soil of an open woods on a north-facing slope of Dupont Mountain revealed a nest chamber of ***seminole***. This chamber contained a nonpendent fungus garden having a volume of approximately 3.75 cc. The upper surface of the garden was contiguous with an edge of the rock when the latter was in its normal position. This uppermost nest chamber was connected by a gallery 2.5 cm. long to the small nest entrance near an edge of the rock and by a gallery 4.7 cm. long to a second chamber which contained a nonpendent fungus garden having a volume of about 6.53 cc. The second chamber had been constructed at a position horizontal with the first and was located at a depth of 4.8 cm. from the soil surface. A third and much larger nest chamber was lateral to the second one and was connected with it by a gallery 3.2 cm. in length. It was at a depth of 9.7 cm. from the soil surface and contained a pendent fungus mass possessing a volume of nearly 49.90 cc. The entire colony was collected in the manner described for that of the other nest. The nest population consisted of 324 workers (including many callows), 57 alate females, 18 dealate females, 26 larvae, and 84 pupae (63 worker and 21 female). No males or male pupae were in the nest and no eggs were segregated from the fungus mass.

It is of interest to note that although the nest of ***seminole*** ordinarily has a circlet or semicirclet of detritus surrounding its entrance, in neither case mentioned in this paper was such a device present. Indeed the writer should in all probability not have found the nests had he not observed foraging workers in one instance or removed the rock in the other. The elevation at which the two flourishing colonies were located does not seem to prevent the establishment and survival of colonies of at least hardy ***seminole*** stock.

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THE CARE AND BREEDING OF LABORATORY ANIMALS, by EDMOND J. FARRIS (Editor). xvi+515 pages, frontispiece plus 174 text figures. John Wiley and Sons, New York. 1950. Price, $8.00.

This work, produced through the collaboration of fifteen specialists in various fields, attempts to give practical rearing methods and procedures for some of the animals more frequently used in experimental work. Those included are the monkey, the rat, experimental mice, the guinea pig, the Syrian hamster, the rabbit, the dog, the domestic cat, ferrets, the opossum, the domestic fowl, reptiles (snakes, lizards, turtles, and crocodilians), Amphibia, laboratory fishes, and *Drosophila*. A final chapter, by W. E. Dove, deals with the control of laboratory pests and parasites of laboratory animals. The usefulness of this work to the entomologist whose teaching or research project requires the rearing of any of the above animals is obvious.—M. T. J.

THE PARASITE COMPLEX OF FURCASPIS OCEANICA LINDINGER[1]

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A survey through the western Caroline Islands including Ulithi Atoll, Yap, and the Palau group showed that the red coconut scale, *Furcaspis oceanica* Lindinger, existed at a low population level. Invariably, the red coconut scale colonies in this area were found to be parasitized by an encyrtid in the genus *Anabrolepis*. These parasites were collected and transported to Saipan, Mariana Islands, where the scale was abundant and without effective natural enemies.

The releases of parasites on Saipan were made in September and November, 1948. The parasites were observed to probe the scales and presumably to oviposit. However, the definite establishment of this parasite on Saipan has not been determined.

A comparative study of specimens of the genotypic species, *Anabrolepis extranea* Timberlake, the oriental species, *A. japonica* Ishii, and *A. bifasciata* Ishii indicated that this parasite of *Furcaspis oceanica* in Micronesia is a new species. It is therefore described as follows.

Anabrolepis oceanica new species

(Figures 1 and 2)

Female.—Head characteristic of genus, subtriangular on lateral view, dorsal and occipital sides of triangular outline nearly equal, facial surface longest; cheeks long; in frontal view head wider than long, outline of eyes and frons forming semicircle; viewed dorsally frontovertex widening posteriorly, occipital ridge with two prominent bristles, each situated near the posterior aspect of the eyes and curving anteriorly toward frontovertex. Ocelli in middle of dorsal part of frontovertex well forward of occipital margin. Mandibles, fig. 2C, apex broad with 2 acute teeth and a broad truncate inner margin. Antennae, fig. 2B, normal for genus, scape very slightly dilated below; pedicel about one-third length of scape, nearly as long as first four funicle segments combined, gradually widening distad, apical width greater than width of following segment; flagellum slightly clavate, first four funicle segments short, transverse, the last two funicle segments distinctly longer than any of the four preceding segments, the sixth segment distinctly the largest of the funicle. Club three-segmented, wider than funicle and approximately of equal length, apex more pointed than round.

[1]Collecting was done on a survey made under the auspices of the Insect Control Committee for Micronesia of the Pacific Science Board, National Research Council, with financial assistance from the Office of Naval Research.

[2]Lecturer in Biological Control and Assistant Entomologist in the Experiment Station, University of California.

Pronotum strongly arcuate; mesoscutum not appreciably convex but rather flat; axillae short, much wider than long, not contiguous at tips; scutellum a little wider than long, sloping sharply downward along lateral margins, the central portion with hexagonal reticulations, scutellum with five pairs of setae, each pair becoming progressively larger and stouter posteriorly; metanotum narrow, nearly obscured by posterior angle of scutellum, a row of three small setae evident on metanotum adjacent to each side of scutellum; propodeum very narrow

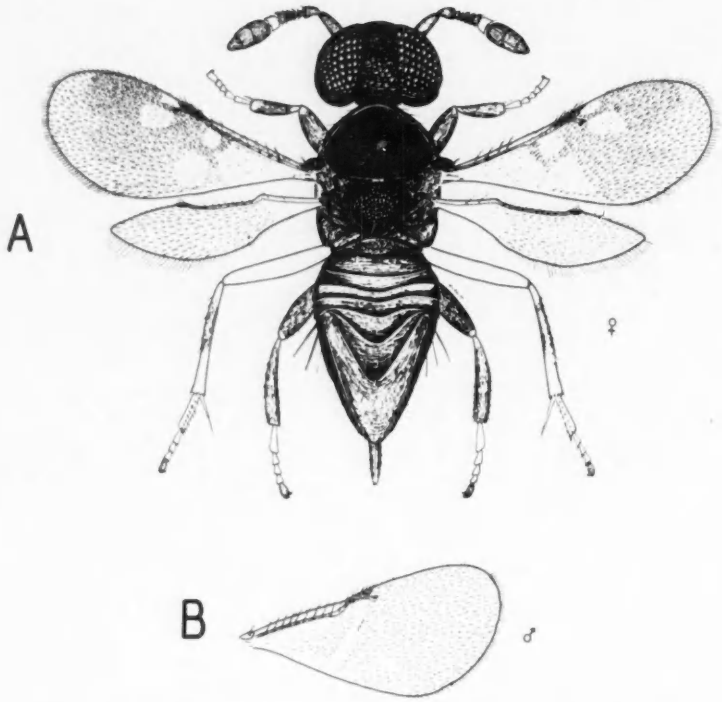

FIG. 1. *Anabrolepis oceanica*, n. sp. A. Adult female. B. Wing of male.

medially, but distinctly enlarging towards sides, spiracles large, conspicuous.

Abdomen long ovate, vibrissal plates on dorsum anterior to middle of abdomen, vibrissae not extending to apex of abdomen. Ovipositor extended for length equal to length of basitarsus of middle legs.

Legs normal for genus, basitarsal segment of middle pair as long as four subsequent segments combined, slightly longer than saltatorial spur, a row of short stout spines on ventral surface of segment. Middle tibiae with apical fringe of short stout spines.

Wings of moderate width, extending appreciably beyond apex of abdomen; submarginal vein bears row of four large setae in basal half of its length, slightly swollen distad; marginal vein stout, bearing thick cluster of setae; stigmal vein nearly one-half length of marginal, enlarged at apex; postmarginal short.

Basic color dark brown to black, but head, dorsum of thorax and abdomen with metallic reflections, a blend of greens, deep blues, and purples depending on incidence of light. Scutellum often with distinct golden highlights. Venter except head, chocolate to dark brown.

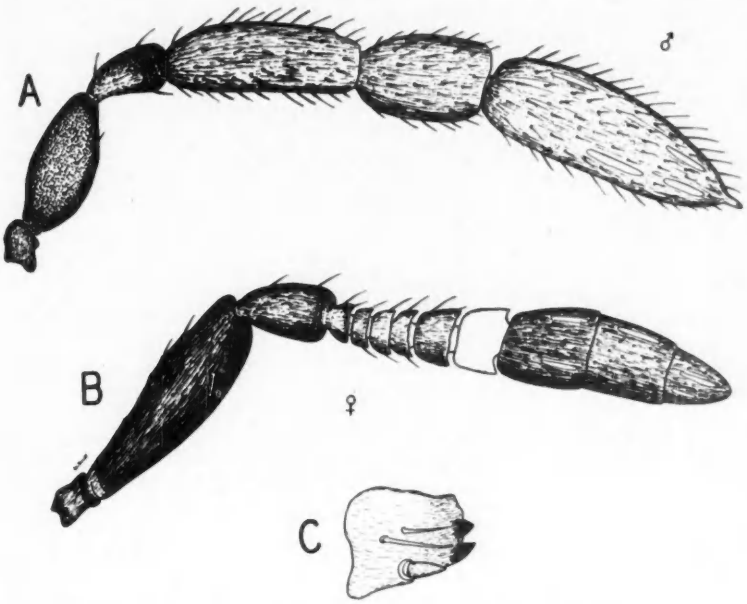

FIG. 2. *Anabrolepis oceanica* n. sp. A. Antenna of male. B. Antenna of female. C. Mandible of female.

Forelegs brown, the tarsi lighter, as are tips of femora and tibiae; middle coxae dark brown, middle femora and tarsi pallid, middle tibiae with band of dark brown; hind legs brown, tarsi lighter, hind femora slightly expanded. Apical tarsal segment of each leg tends to be darker than preceding segments. Antennae black, except sixth funicle segment yellow. Forewings with a large fuscous area interspersed with hyaline spots; the pattern as in fig. 1A, the fuscous area rather indistinctly broken into rays and bands. Posterior wings hyaline.

Male.—Frontovertex very broad, widening both anteriorly and posteriorly, slightly rounded on lateral aspect forming rather soft angles with face and occiput, sculptured with small crowded thimble-like punctures. Pronotum strongly arcuate; mesoscutum flattened, in

some specimens slightly depressed; axillae considerably wider than long, not contiguous at apices; scutellum wider than long, about as female; metanotum and propodeum narrow at apex of scutellum, propodeum strongly enlarging laterally. Specimens mounted in gum damar show mesophragma to be well developed, larger relatively than in female, broadly rounded, extending into abdomen beyond first abdominal segment. Abdomen short.

Antennal scape short, swollen, fig. 2A; pedicel longer than wide, about half length of scape; first funicle segment large, wider than pedicel, longer than scape; second funicle segment wider than preceding segment but shorter, nearly equal to scape in length; club solid, widest antennal segment, longer than combined lengths of scape and pedicel, apex with small papilliform projection. Funicle and club very setaceous.

Wings moderately broad, fig. 1B, oblique hairless streak extending from beneath marginal vein basally toward posterior wing margin. Submarginal vein with numerous stout setae, vein enlarged in distal third; marginal vein very setaceous; post-marginal short; stigmal vein triangularly enlarged at apex. Wing hyaline except for small fuscous area beneath marginal vein.

General body color dark brown to black. Head and thorax with metallic purplish highlights in reflected light. Antennae brown, scape and pedicel darker than funicle and club. Legs brown, darker than those of female, with tips of femora and tibiae light. Tarsi of middle legs pallid, apical segment darker.

Holotype.—Female, Potangeras Islet, Ulithi Atoll, Aug. 20, 1948. (R. L. Doutt). *Allotype.*—Male, Yap, Caroline Islands, Sept. 27, 1948 (R. L. Doutt). *Paratypes.*—5 females and 15 males, Yap, Oct. 1, 1948 (R. L. Doutt); 11 males, Yap, Sept. 27, 1948 (R. L. Doutt); 3 females and 12 males, Babelthuap, Palau Islands, Oct. 7, 1948 (R. L. Doutt); 1 female and 3 males, Ulithi Atoll, Aug. 20, 1948 (R. L. Doutt). All specimens reared from *Furcaspis oceanica* Ldgr.

Holotype and allotype deposited in U. S. National Museum. Paratype series deposited with U. S. National Museum, California Academy of Sciences, and Division of Biological Control, University of California.

Anabrolepis oceanica is most easily distinguished from *A. extranea* Timb., *A. japonica* Ishii, and *A. bifasciata* Ishii by the characteristic wing pattern.

SECONDARY PARASITES

In the Palau Islands, besides the encyrtid *Anabrolpeis oceanica*, a number of specimens of a small aphelinid belonging to the genus *Ablerus* were reared from the same host material. The status of this parasite could not be definitely determined, but it is presumed to be a secondary. It was always found associated with populations of *Anabrolepis oceanica*.

Ablerus palauensis new species

(Figure 3)

Female.—Frontovertex with inner orbital margins arcuately emarginate, greatest width immediately anterior to lateral ocelli, narrowest width at occipital margin, small setae anterior to lateral ocelli near

margin of eyes. Face deeply impressed, antennae originate low on face. Cheeks long, impressed on upper portion immediately beneath eyes. Frontovertex and upper face yellow, eyes and ocelli bright red; a brilliant white band encircling head including occiput, upper cheeks beneath eyes, face above antennal insertions; this white band bordered beneath by a narrow stripe of black. Clypeus, lower cheeks, and region surrounding mouth parts yellow brown. Mandibles, fig. 3C, with two sharp nearly equal teeth and a third truncate.

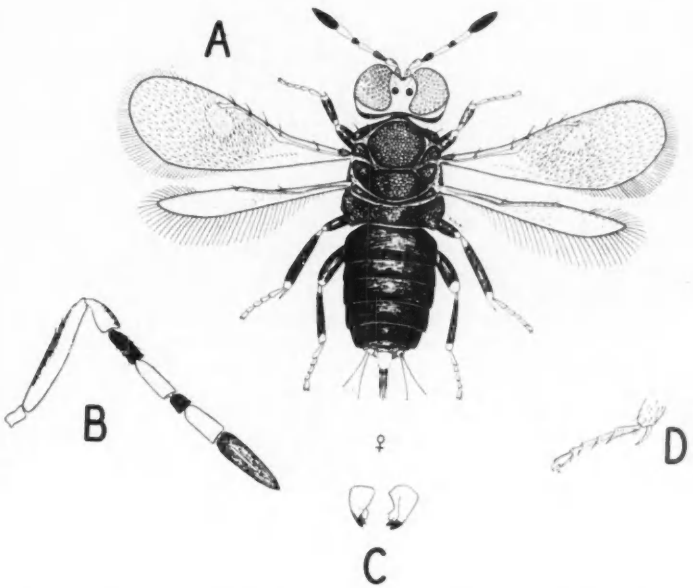

FIG. 3. A. *Ablerus palauensis*, n. sp., adult female. B. Details of antenna. C. Mandibles. D. Foretarsus.

General body color dark brown to black. Dorsum of thorax with blend of greenish and golden reflections; abdomen with purplish metallic luster. Specimens in alcohol appear to have reticulated sculpturing on mesoscutum, scutellum, and propodeum. In slide mounted specimens these reticulations linear and containing small longitudinal striations forming pattern very like a dactylogram.

Pronotum with two setae on each lateral expansion; mesoscutum with two setae, each located near posterior lateral corners; parapsides with two setae; axilla with a single seta; scutellum with two laterally placed, longitudinal rows of three setae; metanotum with two minute setae on each lateral expansion; propodeum with two setae lateral to each spiracle.

Abdomen with faint reticulate sculpturing; area near cercal plates pallid. Mesophragma extends to middle of abdominal length.

Antennal scape long, cylindrical, fig. 3B, length equal to any three funicle segments; pedicel equal in length to first funicle segment, but wider; second funicle segment cylindrical, longest funicle segment; third funicle segment short, subquadrate; fourth funicle segment subequal to first segment, but wider, width equal to pedicel; club solid, pointed, nearly equal to combined lengths of first two funicle segments, with elongate sensorial pits. Small ring joint present between pedicel and first funicle segment. Antennae yellow-brown except funicles 1, 3, club, and dorsal surfaces of scape and pedicel which are dark brown to black.

Forewings with numerous discal cilia, except distinct oval portion beneath stigmal vein with few cilia, nearly bare, fig. 3A. Distinct fumated cross band extending diagonally and apically from beneath marginal vein toward caudal margin. Marginal cilia moderately long. Submarginal vein with triangular expansion near distal portion; marginal vein with three large setae and several smaller setae dispersed throughout its length; stigmal vein slightly enlarged at apex, somewhat as in *Azotus* group. Posterior wings with long marginal cilia, exceeding width of blade; discal cilia concentrated beneath marginal vein, sparse apically except for row near anterior margin; slightly fumated band beneath marginal vein.

Trochanters white; fore and hind coxae black except at apices which are nearly white, middle coxae white. Femora with center band of black, bases and apices white or pallid. Tibiae dark brown to black, lighter at tips; tarsi light brown except apical segment which is dark. Fore tarsi as in fig. 3D, basal segment with a strigil.

Ovipositor and valves extended, valves black with white tips.

Male.—Similar to female with the following exceptions: Antennal club indistinctly two-segmented, transverse septum difficult to see, segments not articulated, nearly fused; first, second, and fourth funicle segments subequal in length, third funicle segment small, nearly quadrate. Antennal segments brown, concolorous, except funicle segments 2 and 4 which are lighter.

Abdomen relatively shorter than in female, approximately equal to length of thorax.

Holotype.—Female, Babelthuap, Palau Islands, Oct. 7, 1948 (R. L. Doutt). *Allotype.*—Male, Babelthuap, Palau Islands, Oct. 7, 1948 (R. L. Doutt). *Paratypes.*—13 females and 1 male, Babelthuap, Palau Islands, Oct. 7, 1948 (R. L. Doutt). All specimens reared from *Furcaspis oceanica*, but associated with *Anabrolepis oceanica*.

Holotype and allotype deposited in the U. S. National Museum. Paratype series deposited with U. S. National Museum, California Academy of Sciences, and Division of Biological Control, University of California.

Ablerus palauensis sp. n. is perhaps best distinguished by the dense wing ciliation and the conspicuous bare oval area beneath the stigmal vein. The coloration of the head should also be an easy diagnostic character. The antennal structure and shorter setae on marginal vein differentiate it from *macrochaeta* Silvestri. The differences in relative

lengths of the antennal segments separate *palauensis* from *magistrettii* Blanchard. The color of the antennae differentiates this new species from *leucopidis* Blanchard. With reference to the key of Australian species (Girault, 1913) *palauensis* appears to belong with the group including *semifuscipennis* Girault, *bidentatus* Girault, and *nympha* Girault, but may be readily separated from these species by the diagnostic characters given above.

From colonies of *Furcaspis oceanica* collected on Ulithi Atoll there emerged specimens of *Marietta carnesi* (Howard). This parasite is probably a secondary, attacking *Anabrolepis oceanica*. *M. carnesi* has a wide distribution having been previously recorded from Japan, China, India, Delaware, and doubtfully California (Compere, 1936). It is known to attack *Comperiella bifasciata* Howard, a primary parasite of disapine scales which is widespread in Micronesia.

SUMMARY

Populations of the red coconut scale, *Furcaspis oceanica* Ldgr., were found to be suppressed effectively throughout the western Caroline Islands by a new species of Encyrtidae described as *Anabrolepis oceanica*. This parasite was transported to Saipan in an attempt to control the coconut scale on that island.

In the western Caroline Islands two supposedly secondary parasites were found to be associated with the populations of *Anabrolepis oceanica*. These were *Marietta carnesi* (Howard) and a new species of Aphelinidae designated as *Ablerus palauensis*.

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Compere, Harold. 1936. Notes on the classification of the Aphelinidae, with descriptions of new species. Univ. of Calif. Publ. in Ent. 6(12): 277–322.

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STUDIES HONORING TREVOR KINCAID, by MELVILLE H. HATCH (Editor). University of Washington Press, Seattle. iii+167 pp. 1950. Price, $2.50.

Though he has relatively few publications to his credit (Dr. Hatch lists 22), Dr. Trevor Kincaid has had a profound influence upon the progress of biological science, both theoretical and applied, in the Pacific Northwest. As a teacher, he has inspired students who have carried on the torch of education and research; as a servant of his community, in a scientific way, he has made valuable contributions; and as a broad and tireless collector he has furnished much material to others for taxonomic research. As partial testimony of this last statement, we note a list of 64 organisms which have been named after him; these include a plant, protozoans, coelenterates, annelids, molluscs, arthropods (including 37 insects), a ray, and two fishes.

The present volume consists of eleven papers by former students and associates of Dr. Kincaid. Three of these papers, by Dr. Hatch, are edvoted to the life and work of Dr. Kincaid and of his predecessor and teacher, Orson Bennett Johnson, and to the Young Naturalists' Society, a pioneer organization consisting mostly of amateurs and founded at the time when Seattle was a frontier village, and in which both Kincaid and Johnson took a very active part.

Only one paper in the present volume deals with arthropod taxonomy: "Conopisthine spiders (Theridiidae) from Peru and Ecuador," by Harriet Exline. —M. T. J.

THE GENUS PYCNOPSYCHE (TRICHOPTERA)

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In our report on the Walker types of Trichoptera in the British Museum, Mosely and I followed an earlier suggestion that it might be well to unite into one genus several North American species of Limnephilidae previously assigned to several genera and differentiated largely by the number of tibial spurs. This paper adds somewhat to the knowledge of these species and confirms the judgment that they should be considered congeneric in *Pycnopsyche* Banks. This genus was described by Banks in 1905 (Trans. Amer. Ent. Soc., 32 : 9), based on *Limnephilus scabripennis* Rambur.

The species of *Pycnopsyche* are, as Trichoptera go, fairly common and conspicuous insects of yellow color with some brown markings, from 15 to 23 mm. in length to the wing tips, occurring as adults in August, September, and October, with a few records in July and November. The larvae also are conspicuous among aquatic insects because of their size and in some species because of a slender stick, sometimes two, or even more, which may be laid alongside the wooden case, projecting beyond the rear end. In the pupal case small stones may replace the wood to some extent, the stick at the end may disappear, and the anterior end is fastened to a submerged stone or often to a submerged branch of a tree or shrub. Not many life histories have been described and even the case-building habits of the various species are not fully known. Larvae of either *P. lepida* or *P. subfasciata* were observed to have the stick attached when the overall length of the case was but 4 or 5 mm. Larvae of *P. gentilis* had cases made of pebbles when observed three or four weeks before pupation and very possibly these have stone cases throughout the larval life. Much may depend on what materials are available.

CHARACTERS COMMON TO THE ADULTS OF PYCNOPSYCHE

Antennae stout, about as long as the wings, yellow or orange in color, sometimes ringed darker, basal joint about equal to the head in length. Head covered with numerous yellow hairs and stouter bristles, the latter arranged in areas often referred to as warts. On either side of the head two such spined areas adjacent to the base of the antenna, a larger one parallel with the posterior margin of the head, and a lunate one posteriorly bordering the eye (figs. 4, 5).

Prothorax with a large area of coarse bristles on either side; on the mesonotum (fig. 8) narrow areas of bristles extend longitudinally on either side of the scutum and scutellum. Legs each with a line of bristles along the coxa, a black spot prominent on the trochanter, the femur almost bare, tibia and tarsus with numerous black spines, hind tarsus with one or more such spines (*P. gentilis* frequently an excep-

tion). Tibial spurs 1-2-2, 1-3-3, or 1-3-4. Wings with surface more or less tuberculate, their shape varying somewhat with the species (figs. 1, 2). Color of the wings yellow to orange, sometimes almost unicolorous but always with brown areas which, in so far as they are present, conform to a common pattern which may include the posterior apical margin, a series of spots in the bases of the apical cells, a transverse band in the middle of the wing, and, less well marked, the posterior margin. One species has prominent round, brown spots on the forewing; in another species the spots are small and not at all conspicuous. Anal area of the hindwings covered with long thin hairs, the amount of the covering differing with the species, more conspicuous in males than in females. Venation as in the figures (figs. 1, 2), the difference between the species not great.

Eighth tergite of the males fairly heavily sclerotized, its dorsal posterior margin often set with short, black spines, the shape and location of these spinose areas being often diagnostic of the species, lower posterior angle of the chitinous shield of this tergite sometimes extended as a hook, point, or rounded knob (figs. 19, 36, 79). Ninth segment strongly sclerotized, its dorsal half often telescoped into the eighth segment; seen from the side it is widest in the middle, tapering dorsally and ventrally (fig. 61). Attached to the dorsal part of the ninth segment there is a paired structure (10 in figs. 61, 63), representing doubtless the tenth segment, consisting ordinarily of a pair of broad lateral pieces (dorsal or superior appendages of McLachlan and others) running mesally into a pair of processes (intermediate appendages), these often curved at the tips; generally a sclerotized area on the surface of the ninth segment connects the tenth segment with the claspers at about the point where the tips of the latter become free, thus the anal aperture is more or less encircled by these structures (fig. 101). Claspers (inferior appendages) in an upright position in relation to the body axis, broadly united to the ninth segment throughout most of their length, the basal part covered with stout bristles; the tips of the claspers, which are free of the ninth segment, variously shaped and often divided (figs. 51, 57, 69, 75). Aedeagus highly characteristic in form, its general structure much the same throughout the genus; arising in a concavity on the dorsal surface are two appendages (titillators) of several types as figured (figs. 13–18).

Female with posterior margin of the seventh ventral segment bordered with fine hairs (fig. 29). Genital opening at the posterior margin of what appears to be the eighth segment; seen from the side its upper and lower lips are conspicuously protruding, the lower lip forming a subgenital plate which may be rounded, mucronate, or lobed, its appearance differing greatly according to the exact line of vision. Dorsally a terminal segment, perhaps a modified ninth and tenth, is sclerotized, sometimes heavily so; seen from above, its rear margin is in many cases slightly cleft (fig. 23). The anal aperture with its surrounding structures differs considerably with the species, often oval in shape (fig. 41), with varying degrees of sclerotization in its margin; in several species the opening is large, almost rectangular (fig. 31). In well-cleared specimens the outline of the spermatheca may be seen through the body wall (figs. 9–12).

RELATIONSHIPS

The genera of Limnephilidae are not readily differentiated, except, as is done in most keys, by the use of a combination of characters which may not be strongly indicative of relationships. For *Pycnopsyche* the most characteristic features are the structure of the aedeagus and the shape and position of the claspers of the male; these latter appendages are flatly joined to the ninth segment for the greater part of their length, the line of fusion remaining well marked. The lower part of the clasper, fused with the ninth segment, is broader from side to side than in the direction of the body axis.

The species of Limnephilidae most closely allied to *Pycnopscyhe* are probably *argus* Harris and *hesperus* Banks which have been listed either in *Astenophylax* or in *Pycnopsyche*, and an undescribed species from Maine given to me by Mr. Nathan Banks. These three species share with *Pycnopsyche* its distinctive type of aedeagus, particularly the subtype whose appendage is a slender stylet (fig. 13). They differ in that they have the line of fusion of the clasper with the ninth segment less well marked, the clasper is not so flatly joined to that segment, and its lower part is without a conspicuous covering of bristles. At least in *argus* (fig. 5) the areas of bristles on the head are more slender. Further, while in *Pycnopsyche* the division of the stem of the vein M in the forewing into M_{1+2} and M_3 is at the level of the middle of the discal cell, in these species it is much nearer to the distal end of that cell (figs. 6, 7). In the three species referred to a cross vein is often, though not invariably, present between Sc and R, of the hindwing (fig. 3); this vein does not occur in *Pycnopsyche*. In the females of the three related species an anal tube (figs. 76, 77, 78) is more strongly developed than in any species of *Pycnopsyche*.

Within the genus *Pycnopsyche* there are few clear indications of subsidiary groupings. The genus *Allegophylax*, set up by Banks for *lepida* and *subfasciata* (and by later addition, *indiana*) is a natural unit agreeing in having spurs 1-2-2, as well as in the structure of the genitalia. The species *aglona*, *limbata*, and *sonso* are strikingly alike in respect of the structures terminating the female abdomen; *limbata* and *sonso* agree in having the mesal arms of the tenth male segment greatly elongated, apparently horizontal in *limbata* (figs. 19, 25), more upright in *sonso* (fig. 26); these appendages are largely fused in the middle line in *sonso* (fig. 32); *limbata* is divergent from all other species in the structure of the ninth segment of the male (fig. 19), and in the form of the appendages of the aedeagus (fig. 14); *gentilis* and *flavata* are similar in respect of the appendages of the aedeagus (figs. 15, 17); *guttifer*, *divergens*, *circularis*, and *rossi* have spurs 1-3-3. But none of these things seems very conclusive.

The more important characters of the species are sufficiently indicated in the keys that follow and in the figures. A few notes, mainly on distribution, are added.

Unfortunately most of the characters used in the keys cannot be readily seen except in specimens that have been expanded and cleared in KOH.

KEY TO MALES OF THE GENUS PYCNOPSYCHE

1. Mesal arms of the tenth segment long and slender, extending well beyond the tips of the claspers either caudally if in a horizontal position or dorsally if vertical (figs. 19, 26) 2
   Mesal arms of the tenth segment inconspicuous or heavy, often more or less hidden by the side pieces of the segment, not long and slender 3
2. Anterior margin of the ninth segment, seen from the side, sharply curved to almost a right angle (fig. 19). Appendages of the aedeagus with basal stem longer than the terminal division which is single and ribbon-like (fig. 14). Mesal arms of the tenth segment separate through most of their length (fig. 25) ..... **limbata**
   Anterior margin of the ninth segment not curved to nearly a right angle. Appendages of the aedeagus terminated by a stylet, not flat, ribbon-like. Mesal arms of the tenth segment fused through most of their length (fig. 32) ..... **sonso**
3. Posterior margin of the eighth tergite laterally produced into a rounded lobe densely covered with short black spines (fig. 36) 4
   Posterior margin of the eighth tergite not produced or, if so, not into a rounded scabrous lobe 7
4. Posterolateral scabrous lobe of the eighth tergite near the ventral margin of that tergite (figs. 33, 36). Appendages of the aedeagus terminated by a group of several bristles (figs. 16, 18) 5
   Posterolateral lobe of the eighth tergite near the middle of that tergite as seen from the side (fig. 42). Appendages of the aedeagus terminated by a single stylet 6
5. Tenth segment with mesal arms heavy and prominent (fig. 33). Main tip of the clasper blunt, with a small inner tooth (figs. 33, 35). Field of spines on the eighth tergite extending across that tergite (fig. 34). Spurs 1–3–4 ..... **aglona**
   Mesal arms of the tenth segment not prominent (fig. 36). Tip of the clasper obtusely pointed (fig. 38). Field of spines on the eighth tergite largely limited to the mid-dorsal region (fig. 37). Spurs 1–3–3 ..... **guttifer**
6. Forewings with many conspicuous, round, brown spots of varying size. Claspers indented or cleft at tip, not running into a sharp point (figs. 44, 48). Spurs 1–3–4 ..... **scabripennis**
   Brown spots on the forewings small and not conspicuous. Claspers ending in a single sharp point (fig. 51). Spurs 1–3–3 ..... **rossi**
7. Tips of the claspers not reaching above the level of the tenth segment. Spurs not 1–2–2 8
   Tips of the claspers long, extending well above the tenth segment (figs. 85, 91). Spurs 1–2–2 12
8. Spurs 1–3–3 9
   Spurs 1–3–4 10
9. Posterior margin of the eighth tergite, seen from above, trilobed (fig. 56). Tips of the claspers divided (fig. 57) ..... **circularis**
   Posterior margin of the eighth tergite not trilobed. Tips of the claspers not divided ..... **divergens**
10. Appendages of the aedeagus stout, terminated by a group of spines (figs. 15, 17) 11
    Appendages of aedeagus slender, terminated by a single stylet (fig. 79) ..... **luculenta**
11. A conspicuous area of black spines in the middle of the rear margin of the eighth tergite (figs. 67, 68) ..... **gentilis**
    No conspicuous area of black spines on the eighth tergite ..... **flavata**
12. Posterior margin of the eighth tergite, viewed from above, with a heavy border of black spines, this border with a distinct mesal notch (fig. 86), **lepida**
    Posterior margin of the eighth tergite with black spines which are segregated most heavily in two roughly triangular areas; no distinct notch in the border (fig. 92) 13
13. Posterolateral margin of the eighth tergite notched but not produced into a hook. Claspers with an abrupt shoulder setting off the slender tip. Aedeagus stocky, the tip of its appendage twice as long as its base (fig. 97) ..... **indiana**
    Posterolateral margin of the eighth tergite commonly produced into a hook (figs. 91, 103). Claspers generally narrowed gradually to the tips (fig. 93). Aedeagus slender, the terminal part of its appendage three times as long as its base ..... **subfasciata**

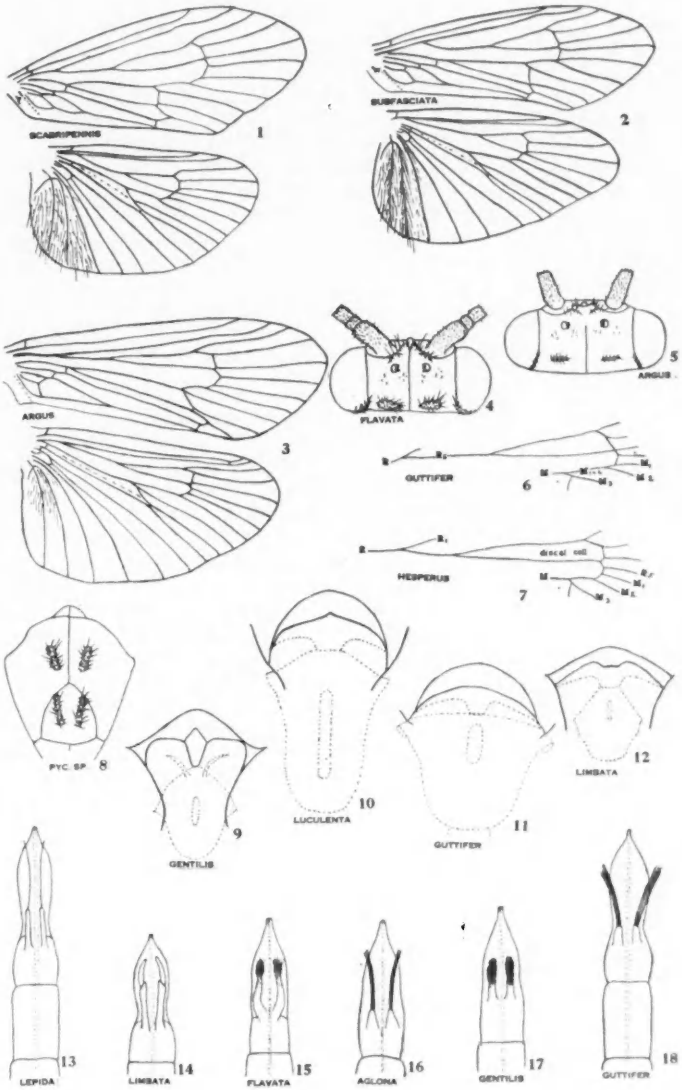
KEY TO FEMALES OF THE GENUS PYCNOPSYCHE[1]

1. Spurs 1–2–2. Terminal segment with either two or three processes arising from the dorsal margin (figs. 89, 90, 95, 96)..... 11
   Spurs not 1–2–2. Terminal segment without dorsal processes..... 2
2. Posterior margin of the terminal segment, seen from above, abruptly concave (fig. 30). Anal aperture broad, roughly rectangular (fig. 31)..... 3
   Posterior margin of the terminal segment, seen from above, not concave. Anal aperture not very broad, not rectangular..... 4
3. Small species, about 15 mm. to the wing tips. Reported from northern states..... **aglona**
   Larger species, 17–20 mm. to the wing tips. Reported from North Carolina..... **sonso**
4. Lower lip of the anal aperture, seen from below, broadly U-shaped, the sides of the opening not sclerotized (fig. 24). Terminal segment, seen from the side, runs out dorsally into a sharp point (fig. 22). Length to wing tips about 15 mm..... **limbata**
   Anal aperture not as above. Terminal segment not sharply pointed. Length to wing tips at least 17 mm..... 5
5. Forewings conspicuously marked with many round, brown spots..**scabripennis**
   No round brown spots on the forewings, or, if present, small and not conspicuous..... 6
6. Spurs 1–3–3..... 7
   Spurs 1–3–4..... 10
7. Dorsal margin of the terminal segment, viewed from the side, curved sharply downward to its apex (figs. 52, 58)..... 8
   Dorsal margin of the terminal segment not curved sharply downward..... 9
8. Subgenital plate with a small middle lobe in its free margin (fig. 60). Lower side of the anal tube sclerotized so as to form an oblique, flat floor beneath (fig. 58)..... **circularis**
   Subgenital plate rounded or mucronate. Floor of the anal tube not sclerotized..... **rossi**
9. Terminal segment very heavily sclerotized, almost square in lateral view. Upper cleft lip extends beyond the remainder of the segment (fig. 64), **divergens**[2]
   Terminal segment not very heavily sclerotized, tapering, the upper and lower lips of the anal tube about equally extended (fig. 39)..... **guttifer**
10. Subgenital plate distinctly trilobed (fig. 72). Between the anal aperture and the genital plate a transverse rectangular field covered with small spines except in the median line (fig. 72)..... **gentilis**
    Subgenital plate with evenly rounded or slightly mucronate margin. Between the anal aperture and the genital plate two rounded areas of small spines (fig. 84)..... **luculenta**
11. Terminal segment with a process at either side dorsally, but none in the mesal line (figs. 89, 90)..... **lepida**
    Terminal segment with a mesal and two lateral processes (figs. 95, 96), **subfasciata, indiana**

[1]The females of *P. aglona* and *P. flavata* are not yet known.
[2]See notes on this species.

EXPLANATION OF PLATE I

Venation of wings: Fig. 1. *P. scabripennis* Rambur. Fig. 2. *P. subfasciata* Say. Fig. 3. *Astenophylax argus* Harris. Dorsal view of head: Fig. 4. *P. flavata* Banks. Fig. 5. *Astenophylax argus* Harris. Detail of venation of forewing: Fig. 6. *P. guttifer* Walker. Fig. 7. *Astenophylax hesperus* Banks. Dorsal view of mesothorax: Fig. 8. *Pycnopsyche* sp. Spermatheca: Fig. 9. *P. gentilis* McLachlan. Fig. 10. *P. luculenta* Betten. Fig. 11. *P. guttifer* Walker. Fig. 12. *P. limbata* McLachlan. Aedeagus: Fig. 13. *P. lepida* Hagen. Fig. 14. *P. limbata* McLachlan. Fig. 15. *P. flavata* Banks. Fig. 16. *P. aglona* Ross. Fig. 17. *P. gentilis* McLachlan. Fig. 18. *P. guttifer* Walker.


SCABRIPENNIS
1
SUBFASCIATA
2
ARGUS
3
FLAVATA
4
ARGUS
5
GUTTIFER
6
HESPERUS
7
PYC. SP.
8
GENTILIS
9
LUCULENTA
10
GUTTIFER
11
LIMBATA
12
LEPIDA
13
LIMBATA
14
FLAVATA
15
AGLONA
16
GENTILIS
17
GUTTIFER
18

Pycnopsyche aglona Ross

Figs. 16, 33–35

1941. *Pycnopsyche aglonus* Ross, Canad. Ent., 73: 18, fig. 6.
1944. *Pycnopsyche aglona* Ross, Bull, Ill. Nat. Hist. Surv., 23: 299 (listed).

This species was described from specimens taken in Ontario (August) and Massachusetts, and is reported also from Maine and from Pinnacle Mt., N. Y. (Sept. 14). Two male specimens taken in northern Wisconsin (Aug. 29) have the basic color pattern of the genus well marked, particularly in the apical part of the forewing.

This species and *limbata* can ordinarily be separated from the others by their small size (about 15 mm.), but small sized individuals occur in other species. The massive dorsal appendages of the male are rather distinctive.

The female of *aglona* has not been described; a female specimen from Norway, Maine, in the Museum of Comparative Zoology at Cambridge, Mass., apparently belonging here, seems to have terminalia of the same type as those of *sonso*.

Pycnopsyche circularis Provancher

Figs. 55–60

1877. *Platyphylax circularis* Provancher, Nat. Canad., 9: 260.
1878. *Platyphylax circularis* Provancher, Petite Fauna Ent. Can., p. 135.
1935. *Stenophylax circularis* Milne, St. N. Amer. Trich. 2: 33, 52.
1944. *Pycnopsyche circularis* Ross, Bull. Ill. Nat. Hist. Surv., 23: 299 (listed).

The male of this species is distinguished by having the posterior margin of the eighth tergite, as seen from above, divided into three spinose lobes; these latter are dorsal rather than lateral and, in the use of the key for the determination of the species, are therefore not likely to be confused with the more lateral scabrous areas shown by males of *guttifer*, *scabripennis*, and other species.

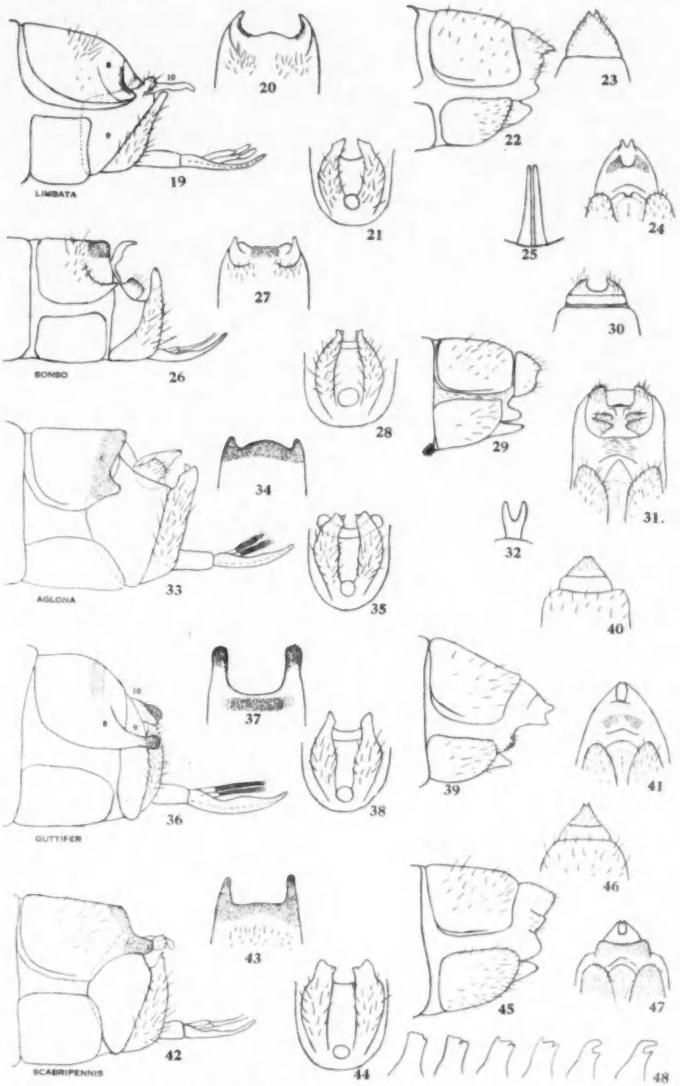
Dr. H. H. Ross kindly lent me a male and a female specimen, collected at Bayfield, Wis., on August 26. I have in addition incomplete specimens from Piseco Lake and Keene Valley, N. Y., also taken in August. Provancher's material was from Quebec and the species is further reported from Maine (Sept. 17), New Hampshire, Massachusetts, and Rhode Island. The male specimen from Wisconsin measures 20 mm. and the female is slightly larger.

Pycnopsyche divergens Walker

Figs. 61–66

1852. *Limnephilus divergens* Walker, Cat. Neur. Brit. Mus., p. 30.
1863. *Anabolia divergens* McLachlan, Ent. Ann., pp. 156, 161.
1864. *Stenophylax divergens* Hagen, Verh. Zool. Bot. Ges. Wien, 14: 855 (listed)
1926. *Halesus dan* Sibley, Jour. N. Y. Ent. Soc., 34: 81.
1926. *Halesus dan* Sibley, Bull. Lloyd Library, No. 27, Ent. Ser., 5: 107, pl. 10, fig. 71.
1934. *Halesus* sp. Betten, N. Y. Mus. Bull., 292: 350, pl. 49, figs. 12, 13.
1935. *Stenophylax dan* Milne, St. N. Amer. Trich., 2: 33, 52.
1940. *Pycnopsyche divergens* Betten and Mosely, Walker types of Trichoptera, p. 146, fig. 73 (*dan* reduced to synonomy).

Originally described from North America, this species is reported only from New York (McLean, Voorheesville, Rochester, Aug. 20–Sept. 22).



Lateral, dorsal, and ventral views of genitalia and terminal structures.

Figs. 19–21, 25. *P. limbata* McLachlan, male. Figs. 22–24. *P. limbata* McLachlan, female. Figs. 26–28, 32. *P. sonso* Milne, male. Figs. 29–31. *P. sonso* Milne, female. Figs. 33–35. *P. aglona* Ross, male. Figs. 36–38. *P. guttifer* Walker, male. Figs. 39–41. *P. guttifer* Walker, female. Figs. 42–44. *P. scabripennis* Rambur, male. Figs. 45–47. *P. scabripennis* Rambur, female. Fig. 48. *P. scabripennis* Rambur, variations in tip of clasper.

It should be said that the determination of the single incomplete specimen from which the figures of the female genitalia were made is open to question. The specimen was taken at Voorheesville, N. Y., on August 30, 1923. It is here assigned to *divergens* largely by the exclusion of other possibilities. The middle and hind legs of the specimen are lacking so that even the partial confirmation by spur formula is not possible.

Pycnopsyche flavata Banks

Figs. 4, 15, 73–75

1914. *Stenophylax flavata* Banks, Can. Ent., 46: 154, pl. 10, figs. 32, 33.
1944. *Pycnopsyche flavata* Ross, Bull. Ill. Nat. Hist. Surv., 23: 299 (listed).

This species is so far reported only from the mountains of North Carolina (July 11, Aug. 18). I have examined the type in the Cambridge Museum of Comparative Zoology and several male specimens lent to me by Dr. D. G. Denning of the University of Wyoming and by the Department of Entomology of the University of Minnesota. The males measure 20 mm. to the wing tips. The female is not described.

Pycnopsyche gentilis McLachlan

Figs. 9, 17, 67–72

1871. *Stenophylax gentilis* McLachlan, Jour. Linn. Soc. London, Zool., 11: 108.
1916. *Eustenace gentilis* Banks, Can. Ent., 48: 122.
1926. *Stenophylax gentilis* Sibley, Bull. Lloyd Library, No. 27, Ent. Ser. 5:107, 218, figs. 100–102, 109.
1934. *Stenophylax gentilis* Betten, N. Y. State Mus. Bull., 292: 342, pl. 48, figs. 3, 4.
1943. *Pycnopsyche perplexa* Banks *nec* Betten and Mosely, Harvard Mus. Comp. Zool., Bull., 92: 346, fig. 35.
1944. *Pycnopsyche gentilis* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 299 (listed).

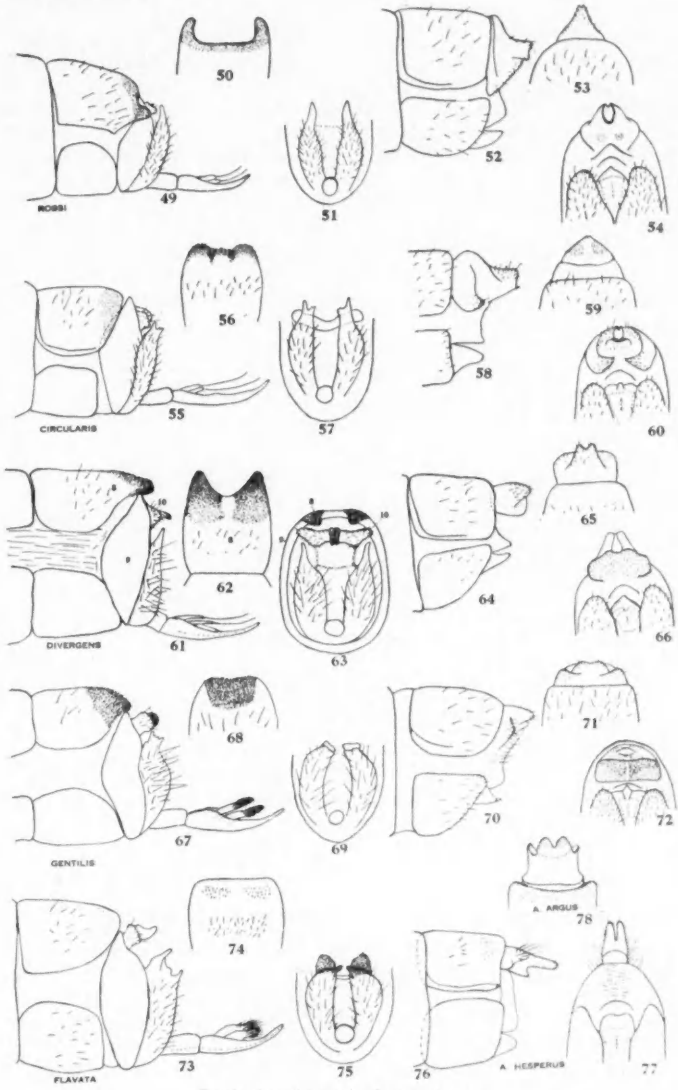
The male of this species is easily recognized by the median scabrous area on the rear margin of the eighth tergite and by the heavy appendages of the aedeagus. The female has the subgenital plate more distinctly trilobed than any other species. The wings of this rather large species are shiny and transparent, the veins of the anastomosis, particularly in its posterior part, are darker than the remainder of the venation and stand out because of the lack of color in the wings.

The species is reported from Nova Scotia, New York (Aug. 22–Sept. 28), from most of the northeastern states, Pennsylvania, New Jersey, North Carolina, and Georgia (Oct. 23).

Pycnopsyche guttifer Walker

Figs. 6, 11, 18, 36–41

1852. *Halesus guttifer* Walker, Cat. Neur. Brit. Mus., p. 16.
1906. *Halesus guttifer* Ulmer, Notes Leyden Mus., 28: 24, figs. 30, 31.
1907. *Pycnopsyche guttifer* Banks, Proc. Ent. Soc. Wash., 8: 122, pl. 9, fig. 22.
1907. *Pycnopsyche similis* Banks, Proc. Ent. Soc. Wash., 8: 122, pl. 9, fig. 25.
1934. *Halesus guttifer* Betten, N. Y. State Mus. Bull., 292: 348, pl. 49, figs. 9–11.
1935. *Stenophylax guttifer* Milne, St. N. Amer. Trich., 2: 33 (*similis* reduced to synonomy).
1938. *Stenophylax guttifer* Ross, Psyche, 45: 41 (male lectotype of *similis* designated).
1940. *Pycnopsyche guttifer* Betten and Mosely, Walker types of Trichoptera, p. 150, figs. 75, 76.
1944. *Pycnopsyche guttifer* Ross, Bull. Ill. Nat. Hist. Surv., 23: 196, figs. 676, 680.



Genital and terminal structures.

Figs. 49–51. *P. rossi* n. sp., male. Figs. 52–54. *P. rossi* n. sp., female. Figs. 55–57. *P. circularis* Provancher, male. Figs. 58–60. *P. circularis* Provancher, female. Figs. 61–63. *P. divergens* Walker, male. Figs. 64–66. *P. divergens* Walker, female. Figs. 67–69. *P. gentilis* McLachlan, male. Figs. 70–72. *P. gentilis* McLachlan, female. Figs. 73–75. *P. flavata* Banks, male. Figs. 76, 77. *Astenophylax hesperus* Banks, female (lateral and ventral). Fig. 78. *Astenophylax argus* Harris, female (dorsal).

This species ranks with ***gentilis*** and ***scabripennis*** as the largest in the genus; as in the latter species the forewing is wide in proportion to length. The scabrous projection of the side of the eighth tergite will readily serve for identification of the male. The species is widely distributed, being reported from Nova Scotia, the northern states as far west as Montana and Wyoming, and also from Tennessee, Georgia, Pennsylvania, and Louisiana. The dates of capture noted for New York State run from July 28 to September 29.

The rearing of specimens collected in the Davidson River near Ecusta, North Carolina confirms the assumption that the two females associated with the male type in the Walker collection (Betten and Mosely, 1940, Walker types of Trichoptera, p. 153) are correctly placed.

Pycnopsyche indiana Ross

Figs. 97–100

1938. *Stenophylax indiana* Ross, Proc. Ent. Soc. Wash., 40: 121, fig. 10.
1944. *Pycnopysche indiana* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 196, figs. 674B, D, E, F, 681A.

The specimens on which the original description is based are from Indiana and Ohio (Sept. 15–Oct. 7). Dr. Ross has lent me a paratype from Ohio and also male specimens from Geogria that seem to be the same. The males are like those of ***subfasciata*** in the dorsal aspect of the eighth tergite but are differentiated by a stockier aedeagus, and the clasper has a more abrupt shoulder setting off the tip than is commonly found in ***subfasciata***. The two species need further study as the characters used may be subject to some degree of variation.

Pycnopsyche lepida Hagen

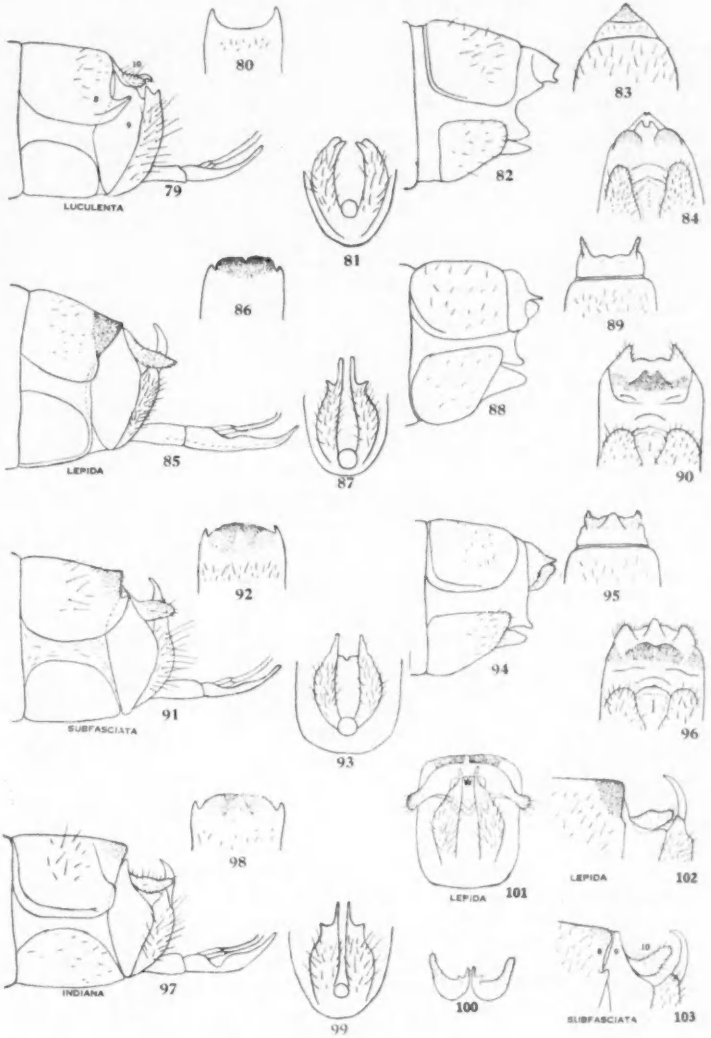
Figs. 13, 85–90, 101, 102

1861. *Enoicyla lepida* Hagen, Syn. Neur. N. Amer., p. 269.
1871. *Platyphylax lepidus* McLachlan, Jour. Linn. Soc. London, Zool. 11: 110.
1916. *Allegophylax lepidus* Banks, Can. Ent., 48: 122.
1934. *Platyphylax lepidus* Betten, N. Y. State Mus. Bull., 292: 350, pl. 50, figs. 4–6.
1935 *Stenophylax lepidus* Milne, St. N. Amer. Trich., 2: 32, 52 (listed as synonym of *subfasciata*).
1938. *Stenophylax lepidus* Ross, Psyche, 45: 41 (lectotype set).
1940. *Allegophylax lepidus* Betten and Mosely, Walker types of Trichoptera, p. 153, figs. 77, 78.
1944. *Pycnopsyche lepida* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 195, fig. 673.

The surest recognition mark of the male of this species seems to be the decided notch in the middle of the posterior margin of the eighth tergite (fig. 86). In ***subfasciata*** and ***indiana***, related species, the scabrous margin of the tergite is continuous and shows two mesal roughly triangular darker areas.

The species is reported from the northeastern states generally, from New York (Aug. 13–Oct. 20), New Jersey, Pennsylvania, Virginia, West Virginia, North Carolina, Georgia, Michigan, Wisconsin, and Illinois.

Dr. J. W. Leonard of the Michigan Institute of Fisheries Research has given me the opportunity of examining a very large number of specimens taken from the Ausable and Marquette Rivers in Michigan and in these the characters here used in the keys appear to be constant.



Genital and terminal structures.

Figs. 79–81. *P. luculenta* Betten, male. Figs. 82–84. *P. luculenta* Betten, female. Figs. 85–87. *P. lepida* Hagen, male. Figs. 88–90. *P. lepida* Hagen, female. Figs. 91–93. *P. subfasciata* Say, male. Figs. 94–96. *P. subfasciata* Say, female. Figs. 97–99. *P. indiana* Ross, male. Fig. 100. *P. indiana* Ross, tenth segment, dorsal. Fig. 101. *P. lepida* Hagen, male (caudal). Fig. 102. *P. lepida* Hagen, male, tenth segment (lateral). Fig. 103. *P. subfasciata* Say, male, tenth segment (lateral).

Pycnopsyche limbata McLachlan

Figs. 12, 14, 19–25

1871. *Stenophylax limbatus* McLachlan, Jour. Linn. Soc. London, Zool., 11: 108, pl. 2, fig. 2.
1916. *Eustenace limbatus* Banks, Can. Ent., 48: 118, 122.
1934. *Stenophylax limbatus* Betten, N. Y. State Mus. Bull., 292: 344, pl. 48, figs. 5, 6.
1935. *Eustenace limbatus* Milne, St. N. Amer. Trich., 2: 50 (genotype of *Eustenace*).
1944. *Pycnopsyche limbata* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 299 (listed).

This is a small, rather well marked species that differs from all the others in having the anterior margin of the ninth male segment sharply angled and also in that the appendages of the aedeagus are flat at the distal end, not tipped with a stylet or with spines. It is reported from New York (July 30–Sept. 17), Rhode Island, the northeastern states generally, and from Quebec, Nova Scotia, Newfoundland, and Ontario.

Pycnopsyche luculenta Betten

Figs. 10, 79–84

1934. *Stenophylax luculentus* Betten, N. Y. State Mus. Bull., 292: 345, pl. 48, figs. 7–12, pl. 49, figs. 1–4.
1944. *Pycnopsyche luculenta* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 196, figs. 677 C, E, 679 B, C.

This is one of the larger species (19–20 mm.). It is reported from New York (Aug. 2–Sept. 21), Maine, New Hampshire, Massachusetts, Pennsylvania, North Carolina, Indiana, and Wisconsin.

Pycnopsyche rossi n. sp.

Figs. 49–54

Color brownish yellow; eyes, a spot on each trochanter, and the spines on the legs, black, as in other species in the genus. Forewings with apical margin of dark brown beginning with cell R_3 and extending around to the tips of the anal veins; the brown color follows along Cu_1 toward the base of the wing; dark spots also in the bases of some of the apical cells and a dark patch runs transversely across the middle of the wing into the discal cell, enclosing the bulla on the main stem of M. Many minute brown spots on the wing surface, not conspicuous as in *scabripennis*.

Male genitalia like those of *aglona*, *guttifer*, and *scabripennis* in having the lateral margin of the shield of the eighth tergite produced into a rounded scabrous point; an area of black spines is continuous along the posterior margin of the eighth tergite, not limited to the mid-dorsal area as in *guttifer*; the appendages of the aedeagus of the type common to *scabripennis*, *luculenta*, and other species, the slender stylet at the end about two times the length of its base. The female has the terminal segment of the abdomen sclerotized, its dorsal margin, as seen from the side, curved downward sharply (fig. 52); the apical cleft in the margin of this segment is very small.

Length, male and female, 17 mm. Tibial spurs 1–3–3.

The holotype male, the allotype, and a female paratype, all taken at McCann Spring, Wolf Lake, Illinois, on October 6, 1947, are deposited in the collection of the Illinois State Natural History Survey at Urbana, Illinois. Dr. H. H. Ross kindly placed these specimens at my disposal and suggested that their description be included in this paper.

Pycnopsyche scabripennis Rambur

Figs. 1, 42–48

1842. *Limnephilus scabripennis* Rambur, Hist. Nat. Insect. Neurop, p. 488.
1852. *Neuronia antica* Walker, Cat. Neur. Brit. Mus., p. 9.
1861. *Hallesus scabripennis* Hagen, Syn. Neur. N. Amer., p. 265 (*antica* reduced to synonomy).
1905. *Pcynopsyche scabripennis* Banks, Trans. Amer. Ent. Soc. 32: 9 (genotype).
1907. *Pycnopsyche scabripennis* Ulmer, Cat. Coll. Zool. Selys Longchamps, 6: 26, figs. 45, 46, pl. 2, fig. 8.
1907. *Pycnopsyche scabripennis* Ulmer, Gen. Insect., Fasc. 60, pl. 4, fig. 28, pl. 33, fig. 1.
1921. *Pycnopsyche scabripennis* Lloyd, Bull. Lloyd Library, 21: 60, figs. 88–95 (immature stages).
1926. *Pycnopsyche scabripennis* Sibley, Bull. Lloyd Library, 27: 108, 219, pl. 12, fig. 95 (immature stages).
1934. *Stenophylax scabripennis* Betten, N. Y. State Mus. Bull., 292: 345, pl. 49, figs. 5–8.
1940. *Pycnopsyche antica* Betten and Mosely, Walker types of Trichoptera, p. 145, fig. 72.
1940. *Pycnopsyche perplexa* Betten and Mosely, l. c., p. 149, fig. 74.
1943. *Pycnopsyche scabripennis* Banks, Bull. Mus. Comp. Zool., 92: 344, fig. 42.
1943. *Pycnopsyche antica* Banks, l. c., p. 344, figs. 30–32.
1943. *Pycnopsyche minima* Banks, l. c., p. 345, figs. 38, 39.
1943. *Pycnopsyche conspersa* Banks, l. c., p. 345, figs. 45, 46.
1944. *Pycnopsyche antica* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 196, figs. 678 C, E, 683 A.

A satisfactory analysis of the *scabripennis* complex still awaits further collection and rearing of specimens. The Rambur type is a female without abdomen, recognizable by the heavily spotted wings. The type of *antica* is also a female. Betten and Mosely doubtfully set off *perplexa* because in the female type specimen the dark spots on the wings are small and less conspicuous than in *scabripennis* generally. Banks separated *minima* mainly by its size, and *conspersa* by the shape of the tip of the clasper. With respect to the character just mentioned it may be noted that there is variation in the extent to which the tip is divided (fig. 48) and the appearance differs greatly with the angle of vision. My judgment remains tentative to the effect that the forms designated *antica*, *perplexa*, *minima*, and *conspersa* will not prove to be of full specific standing.

As *scabripennis* the insect is reported from Quebec, the eastern states as far south as Georgia, and from as far west as Michigan.

Pycnopsyche sonso Milne

Figs. 26–32

1933. *Allegophylax subfasciata* Carpenter *nec* Say, Psyche, 40: 34.
1935. *Stenophylax sonso* Milne, St. N. Amer. Trich., 2: 32.
1944. *Pycnopsyche sonso* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 299 (listed).

The male of this species is easily recognized by the long mesal arms of the tenth segment, fused except at the tip and extending above the lateral pieces of the segment (figs. 26, 32).

Listed from North Carolina and Tennessee, August, September. In a considerable number of specimens reared from the Davidson River in the Pisgah National Forest the dates of emergence range from September 19 to September 30.

Pycnopsyche subfasciata Say

Figs. 2, 91–96, 103

1824. *Phryganea subfasciata* Say, Narrative of Long's Expedition, 2: 308.
1828. *Phryganea subfasciata* Say, Amer. Ent., 3, pl. 44.
1859. *Phryganea subfasciata* Say, Complete Writings, p. 97, pl. 44, fig. 3.
1861. *Enoicyla subfasciata* Hagen, Syn. Neur. N. Amer., p. 269.
1871. *Platyphylax subfasciatus* McLachlan, Jour. Linn. Soc. London, Zool. 11: 110.
1907. *Platyphylax subfasciatus* Ulmer, Coll. Zool. de Selys Longchamps, 6: 25, figs. 40–44.
1907. *Platyphylax subfasciatus* Ulmer, Gen. Insect., Fasc. 60, pl. 33, fig. 4.
1916. *Platyphylax subfasciatus* Vorhies, Trans. Wisc. Acad. Sc., Arts and Letters, 16: 678, pl. 56, figs. 5–7.
1916. *Allegophylax subfasciatus* Banks, Can. Ent., 48: 118, 122.
1934. *Platyphylax subfasciatus* Betten, N. Y. State Mus. Bull., 292: 351, pl. 50, figs. 1–3.
1935. *Stenophylax subfasciatus* Milne, St. N. Amer. Trich., 2: 52 (*lepida* listed as synonym).
1936. *Stenophylax subfasciatus* Elkins, Ann. Ent. Soc. Amer., 29: 669, pl. I, fig. 4, pl. 5, fig. 2.
1944. *Pycnopsyche subfasciata* Ross, Bull. Ill. State Nat. Hist. Surv., 23: 194, 195, figs. 635, 640, 675, 682 (neotype described).

The nearest allied species is *indiana* from which it differs in that the aedeagus is a little less stocky and the claspers are often narrowed more gradually to the tips. The species *subfasciata* is like *indiana* and differs from *lepida* in that the posterior margin of the eighth segment does not have a distinct mesal notch. The notch in the lateral margin of the tergite tends to be more distinctly hooked than in the two related species (figs. 91, 103).

The species has been reported from Ontario, Manitoba, Ontario, New York (July 19–Sept. 26), Massachusetts, Pennsylvania, West Virginia, Michigan, Wisconsin, Illinois, South Dakota, and Wyoming.

THE BIOLOGY OF DROSOPHILA, by M. Demerec (Editor). x+632 pages, 251 figures. John Wiley and Sons, New York. 1950. Price, $10.00.

Even our best-known insects, the house fly, the honey bee, the silk worm, and the pomace fly, are not as thoroughly known as we would like to believe. Consequently, when the present work was projected, ten years ago, it became necessary to institute research programs to fill important gaps in our knowledge of the familiar laboratory animal of the genetecists. To accomplish this, seven collaborators, Dietrich Bodenstein, Kenneth W. Cooper, G. F. Ferris, Albert Miller, D. F. Poulson, B. P. Sonnenblick, and Warren P. Spencer, were invited to prepare the work under the editorship of Dr. Demerec. The resulting volume should serve as an important reference on the fields covered, namely, the spermatogenesis, embryology, morphology and development of the postembryological stages, external and internal morphology of the adult, and methods of collecting and rearing, for *Drosophila melanogaster*. The phases of biology treated are mainly those that will interest the geneticist; but the subject matter, both in reference to this species and for comparison with other forms, will be of great interest to entomologists.—M. T. J.

NOTES ON THE PHLEBOTOMUS OF PANAMA

(Diptera, Psychodidae)

VI. Phlebotomus shannoni Dyar and Related Species[1]

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The sandflies discussed in this paper form an ill defined group mostly lacking any outstanding peculiarities. Their grouping together is for convenience and does not imply any phylogenetic significance. The males are characterized by having four major spines but no accessory setae on the style; no basal, median or apical tufts of setae on the coxite; the parameres simple, without forks, branches or modified setae; the lateral lobes relatively long and without modified spines; the aedeagus and genital filaments of conventional form, the latter from two to four times as long as the pump and with simple tips. The flared anterior end of the plunger of the sperm pump is rather small.

Females have been associated by breeding in two species and on other good evidence in two further species. In *Phlebotomus shannoni* Dyar, *P. punctigeniculatus* Floch and Abonnenc and *P. pestanai* Barretto and Coutinho, the cibarium bears four to eight horizontal teeth, the pharynx is unarmed and the spermathecae are shaped like stout sausages with short to long individual ducts joining a common duct of moderate length.

Both sexes have rather long palpi, the combined first and second segments subequal to the third, the fourth much shorter and the fifth longest. The fifth segment may or may not exceed in length the first three segments combined. The first flagellar segment of the antennae exceeds in length any palpal segment and may exceed any two segments. The ascoids are moderately long, from one-half to as long as their respective segments, except in the case of the first flagellar segment. In all those species where these structures have been described, the ascoids are biramous, bearing a proximally directed branch which may be short or exceed the base of the segment. Newstead's scales are borne on the dorsal inner aspect of the third palpal segment, being numerous and spread over the central two-thirds of the segment in those species we have examined. The second sternite is deeply divided,

[1]This work was initiated under a contract, recommended by the Committee on Medical Research, between the Office of Scientific Research and Development and the Gorgas Memorial Laboratory, and was done, in part, under a contract between the Army Medical Research and Development Board, Office of the Surgeon General, and Gorgas Memorial Laboratory.
Cost of publication is paid by the Gorgas Memorial Institute.

though often fused apically, in the four species we have examined, being similar in all to the figures of ***shannoni*** given here.

Those members of the group which we have seen are conspicuously long-legged, a character of practical utility in dealing with live specimens or in sorting out lots for identification. The tibiae are particularly long compared with the femora. The ratio of tibia to femur for the hind legs ranges from 2.0 to 2.2, which was approached but not equalled by only three species in the random sampling of 25 species from other groups, in which this ratio ranged from 1.3 to 1.95.

Of described species, the following agree with the above definition in both sexes: *P.* ***shannoni***, ***punctigeniculatus*** and ***pestanai***. Males of ***texanus*** Dampf and ***minasensis*** Mangabeira can perhaps be placed here. The female of ***texanus*** differs in having globose spermathecae and about 19 teeth in the cibarium, while the female of ***minasensis*** is as

TABLE OF MEASUREMENTS IN MICRA

	shannoni 10 males		*punctigeniculatus* 9 males		*undulatus* 5 males		*volcanensis* 8 males	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Antenna III	424	264	308	240	332	304	480	404
Palp I–II	200	128	152	128	148	140	200	180
Palp III	156	100	128	96	116	108	176	140
Palp IV	76	48	96	48	68	60	84	72
Palp V	280	180	208	184	208	160	240	212
Wing length	2844	1580	2010	1740	1800	1692	2880	2610
Alpha	828	414	414	252	396	324	810	720
Beta	378	234	306	234	342	234	504	432
Gamma	360	162	342	216	288	198	414	270
Delta	216	108	90	—18	72	36	198	90

yet unrecognized. *P.* ***maracayensis*** Nunez-Tovar may have belonged in this group, but the description is inadequate and the types are no longer in existence. *P.* ***lanei*** Barretto and Coutinho, of which we have material, differs in having a somewhat elongate style, with all spines inserted well distally of the middle. The parameres are also of a different type. The proximal projections of the ascoids are very short and inconspicuous and the spermathecae are annulate.

In addition to the species discussed here, we have female specimens of two other species which may belong here. Both have long proximal branches on the ascoids, with wing and palpal measurements similar to ***shannoni***. Spermathecae of one of these also have the evanescent envelope of ***shannoni***, though they are differently shaped and with wholly separate ducts. The other has annulate spermathecae. We postpone their description in the hope of securing males.

Phlebotomus shannoni Dyar

(Plates I–II, figs. 1–14, Plate IV, figs. 29–30)

1929, Amer. Jour. Hyg., 10(1): 121, figs. 3–4 (♂; Cano Saddle, Gatun, Canal Zone). Barretto 1947, Arq. Zool. S. Paulo, 5(4): 222–223.

Phlebotomus limai Fonseca 1935, Mem. Inst. Butantan, 10: 61, figs. 1–3 (♀; Serra de Cantareira, São Paulo, Brasil).

Phlebotomus bigeniculatus Floch and Abonnenc 1941, Inst. Pasteur Guyane, Pub. 28, pp. 4–7, figs. 2–3 (♂, ♀; Cayenne, French Guiana).

Barretto (*l.c.*) has given complete references, which need not be repeated here. We have examined the types at the United States National Museum. The species has been bred in Brasil and the early stages described (Barretto 1941) so there is no question as to the association of the sexes.

We give here figures of the male genitalia, head, wing, palpi, antennae, female cibarium and spermathecae, second sternites of both sexes, together with measurements of a series of Panama specimens.

An outstanding character of the spermathecae, so far noted in only one other sandfly, the undescribed species mentioned above, is the presence of a sharply outlined, refractive envelope of uniform thickness, which can always be seen in phenol (figs. 11–12). It gives the impression of a melon cut longitudinally. The envelope may (fig. 11) or may not (fig. 12) enclose the "head" bearing the minute hairs (glandular ducts?). The envelope disappears with treatment in KOH. Tissue walls of varying thickness and degrees of visibility have also been noted in a number of other species surrounding not only the spermathecae but the ducts as well (*e.g.*, *vespertilionis*, Fairchild and Hertig 1947, Pl. I, fig. 2). In none, however, is this feature as constant and conspicuous as in *shannoni*.

The second palpal segment may bear one to three Newstead's scales on its distal end, in addition to those figured for the third segment. The pharynx, though classed as "unarmed," bears numerous very fine teeth, visible only at high magnification. This is also true of many species we have examined which do not have an obvious armature, so the term is relative.

We have examined and identified 221 males and 121 females from Panama. These were taken in 103 collections from 35 localities scattered throughout the country from sea level to 4600 feet elevation. There appears to be little seasonal variation in abundance, our material having been taken in every month of the year, ranging from four collections in October to nineteen in January. This variation probably reflects the amount of collecting done rather than the abundance of the species. The great majority of the collections (74) of this species come from crevices between the buttressed roots of forest trees, hollow trees containing bats (15) and hollow trees without bats (10). Six collections from light traps yielded this species; it has been taken twice in rock crevices and once each in an animal-baited stable trap, on an oiled paper trap on a tree trunk, and resting on a tree trunk. We have never taken it in an animal burrow, and a rather small proportion of the females have been engorged with blood. We do not know its preferred hosts. It is reported to bite man and domestic animals rarely in Sao Paulo, Brasil, in the forest, but to refuse both experimentally (Barretto 1943, Fonseca 1935, Galvao and Coutinho 1940).

Rozeboom (1944) reports it as biting man in the southern United States. In Panama we have no evidence of its biting man or, with the single exception of a specimen from a horse-baited mosquito trap, of its attacking the larger domestic animals.

In general, the species is not a dominant one, being usually outnumbered in collections from buttresses by ***trinidadensis*** Newst. and from bat trees by ***vespertilionis*** F. and H. Most of the collections consist of one or two specimens, with rarely over a dozen taken at a single place and time.

Aside from the Panama material, we have seen specimens from Georgia and Florida (reported by Rozeboom, 1944, as far north as North Carolina), six localities in Costa Rica, Colombia, French Guiana, Brasil, Paraguay and Argentina. One of us (M. H.) during intensive forest collecting in Paraguay, March to May, 1950, obtained 12 male and 8 female ***shannoni*** out of a total of nearly 2000 sandflies so far identified. Three females were taken on a horse or burro (not determined whether actually biting or not), the others in a Shannon light-trap, hollow trees, buttresses or on a castor-oil paper trap. The characteristic envelope of the spermathecae was noted in phenol. The seven mounted males all had the typical ***shannoni*** distribution of setae on the parameres. In comparisons made in the field with mounted specimens from Panama no differences could be noted.

P. abonnenci (Floch and Chassignet, 1947, Inst. Pasteur Guyane, Pub. 157, pp. 1–3, ♂) appears to us to be but a variant of ***shannoni***. Among several hundreds of ***shannoni*** examined we have found a fair number of specimens which agree closely with Floch and Chassignet's description. In any case, almost the sole difference from ***shannoni*** concerns the number of setae on the dorsal surface of the parameres. In typical ***shannoni*** they cover the distal half (fig. 1) but vary in a continuous series to a few setae near the tip (figs. 29–30). The latter forms have always been taken in company with ***shannoni***. Soon after the discovery of the second sternite as a taxonomic character, it was noted that in ***shannoni*** they are deeply divided but often fused apically (Hertig and Fairchild 1950, fig. 4). It was hoped that this might aid in determining whether we were dealing with more than one species. About that time we received one lot with over twenty males, about half of which had the setae limited to the tips of the parameres. There was no correlation whatsoever between the open or closed sternites and any particular distribution of the setae. We are inclined to regard our material as all ***shannoni***.

Through the kindness of Dr. Floch we have been able to examine a specimen of ***abonnenci*** from French Guiana. It agrees in all respects with our Panama material.

Phlebotomus punctigeniculatus Floch and Abonnenc

(Plate III, figs. 15–23)

1944 (July), Inst. Pasteur Guyane, Pub. 81, pp. 5–8, fig. 3. (♂, ♀; near Cayenne, French Guiana. In crevices in trees.) Barretto 1947, Arq. Zool. S. Paulo, 5(4): p. 220.

Phlebotomus christophersoni Damasceno and Causey 1944 (October), Mem. Inst. Oswaldo Cruz, 41(2): 347–349, Pl. 4, figs. 17–21; Pl. 5, fig. 25 (♂; States of Para and Amazonas, Brasil, in hollow trees.) Barretto 1947 (l.c.), p. 193.

The shape of the paramere as figured by the above authors differs considerably, but our material shows both conditions, depending on whether the tip is flattened out or curved inwards. In balsam mounts the tip is generally curved inwards, as shown in our figure. In phenol or aqueous media the tip is generally not recurved, as shown by Floch and Abonnenc. Measurements and other structures seem to agree closely, the short delta and structure of the ascoids being especially characteristic. Floch and Abonnenc in their latest key (1947) separate *punctigeniculatus* from *christophersoni* on small differences in the relative lengths of palpal segments and genital filaments, but we do not believe these are adequate in the present case.

The proportions of the head and distribution of Newstead's scales are essentially the same as in *shannoni*. The second sternites are also substantially the same. Only two of our specimens, both males, are mounted so that the sternites can be seen well. The one figured (fig. 20) is divided and open, while the other is fused apically.

We have examined a total of 40 males and 11 females of this species from Panama and the Canal Zone. All were collected at three localities, Chorrera, Juan Mina, and Chiva Chiva. The Chorrera station was a very large hollow espavé tree (*Anacardium excelsum*) containing numerous bats, growing on the steep banks of a stream in heavy gallery forest. The exposed roots of this tree were hollow and yielded most of our specimens. A few were taken in a smaller hollow tree with bats nearby. The Juan Mina and Chiva Chiva localities were also large hollow espavé trees with bats, and although both have been visited fairly regularly, *punctigeniculatus* has been taken at Juan Mina only five times in six years, and only once at Chiva Chiva. The Chorrera station has yielded specimens eight times, on nearly every visit. Specimens have been secured in March, April, May, July, October and December.

Phlebotomus undulatus sp. nov.

(Plate IV, figs. 24–28)

Male.—Genitalia as figured. Aedeagus short, triangular. Pump and genital filaments about as long as coxite and style, the filaments 2.5 to 3 times as long as the pump, their tips not recurved. Ascoids as in *shannoni*, with long proximal prolongations. Cibarium without visible horizontal teeth, the chitinous arch distinct, apparently as in *shannoni*. Pharynx unarmed. Newstead's scales appear to be similar in number and distribution to *shannoni*, while we can not see the structure of the second sternite in any of our mounts.

Holotype male, slide no. 406, near Esquintla, Guatemala, 25 May, 1945, in buttresses of large trees along roadside. Fairchild and de Leon colls.

Paratypes, two males, same data; three males, between Esquintla and San José, Guatemala, 3 June, 1945, in buttresses and hollow trees along roadside. Fairchild and de Leon colls.

This species is very close to *shannoni*. It differs in having the internal basal spine of the style inserted on a level with or proximally to the external basal spine, instead of distally as in *shannoni*, in the

relatively long lateral lobes, and in having the setae on the paramere longer, more numerous and with a reverse curve in the middle. No females were secured. The name refers to the waved or undulant hairs of the paramere. Although this character might seem quite a trivial one, it is well marked in all our specimens, which are otherwise also quite uniform.

Phlebotomus volcanensis sp. nov.

(Plate V, figs. 31–36)

Male.—A large pale brownish species, the head and mesonotum rather dark. Genitalia as figured. Genital pump and filaments slightly longer than coxite and style, the filaments about 2.5 times as long as the pump, their tips slightly hooked. Cerci as in *shannoni*. Ascoids with long proximal prolongations, essentially as in *shannoni*. Cibarium without visible horizontal teeth, but with fairly numerous small vertical teeth. Chitinous arch well developed, its relative position similar to that of *shannoni*. Pharynx unarmed. The head proportions and the distribution of Newstead's scales also appear similar to *shannoni*, though none of our specimens show the latter well. The second sternite is mounted laterally in our series, but can be seen to be of the same type as in *shannoni*.

Holotype male, slide no. 652, and *Paratypes*, seven males, slides nos. 648, 649, 653–657, Cerro Punta, Volcán de Chiriquí, ±6500 ft. elev., Chiriquí Province, Panama, 22 to 27 May, 1946. Galindo and Fairchild colls. The specimens were taken in hollow trees and buttresses in heavy forest around Finca Carinthia. Types to be deposited in the Museum of Comparative Zoology and the United States National Museum. These were the only *Phlebotomus* seen at this locality and were distinctly rare. No females were taken.

P. volcanensis appears to belong to the *shannoni* group on the structure of genitalia and ascoids. It differs from the other species treated here in its considerably larger size and in the structure of the paramere. Further comparisons must await the discovery of the female.

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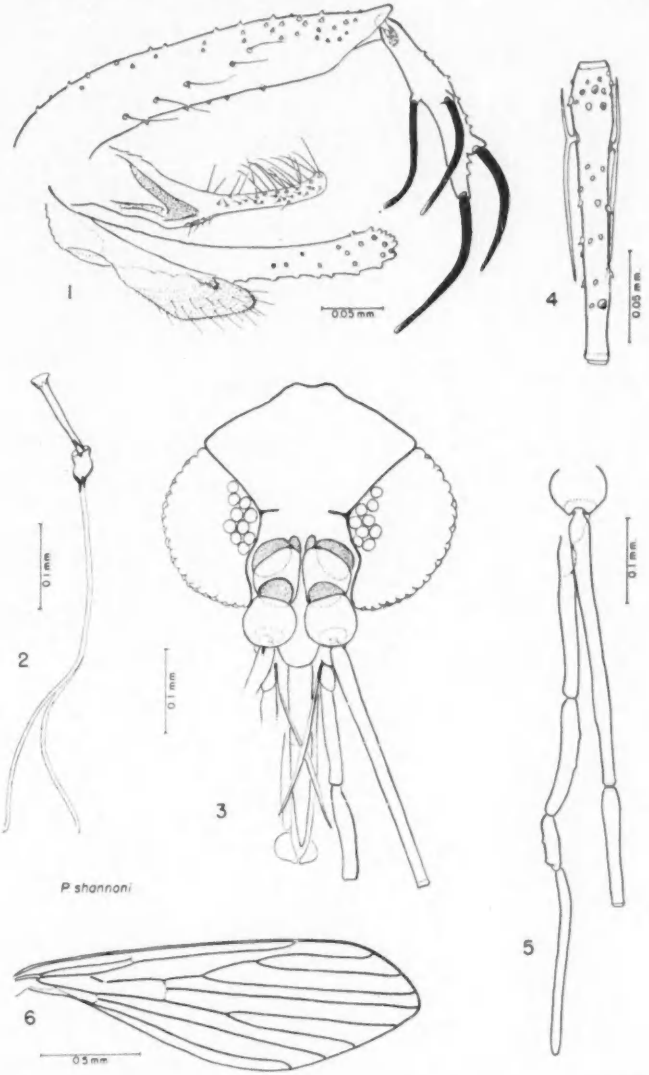
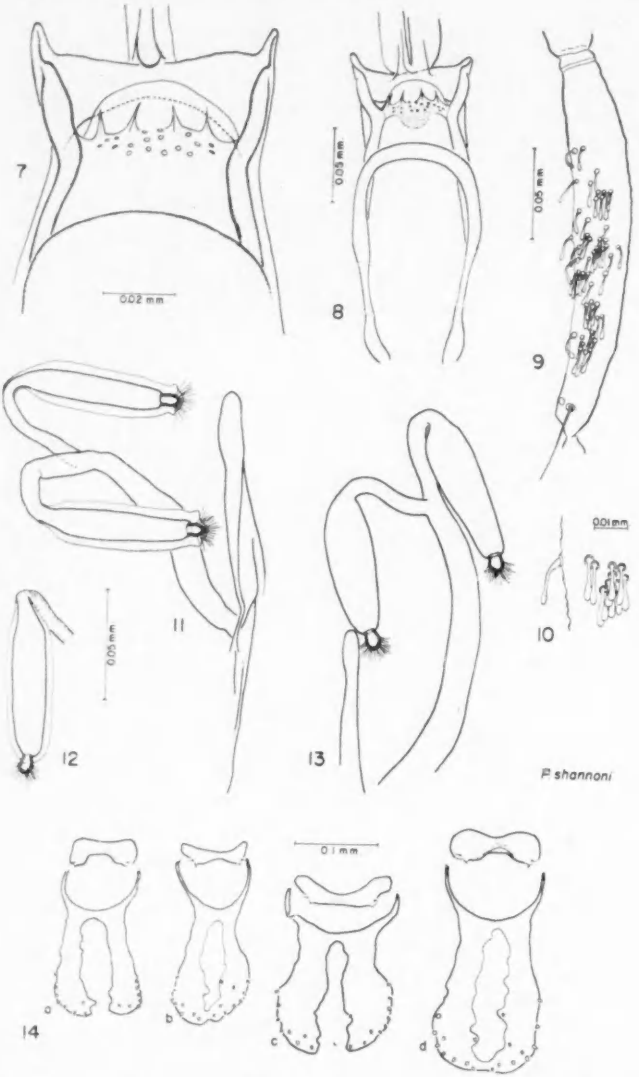


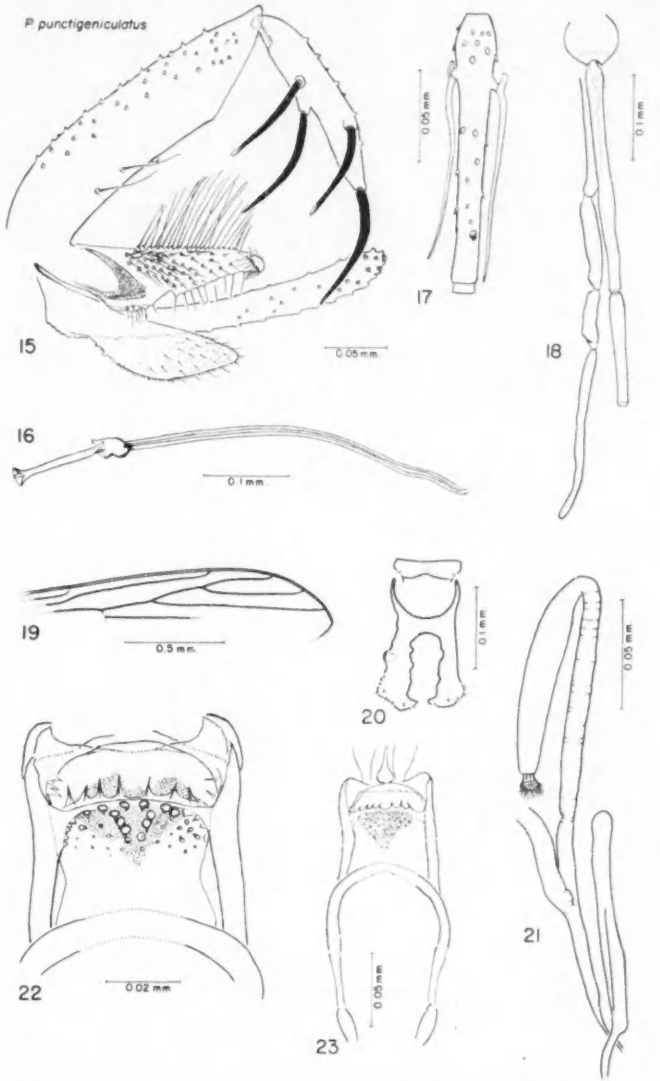
Phlebotomus shannoni. All figures are of males. FIG. 1. Male genitalia, inner aspect. FIG. 2. Genital filaments and pump. FIG. 3. Head, dorsal aspect. FIG. 4. Antennal segment IV, showing ascoids. FIG. 5. Palp and basal antennal segments. FIG. 6. Wing.

See also Plate IV, figs. 29–30, for variant form.

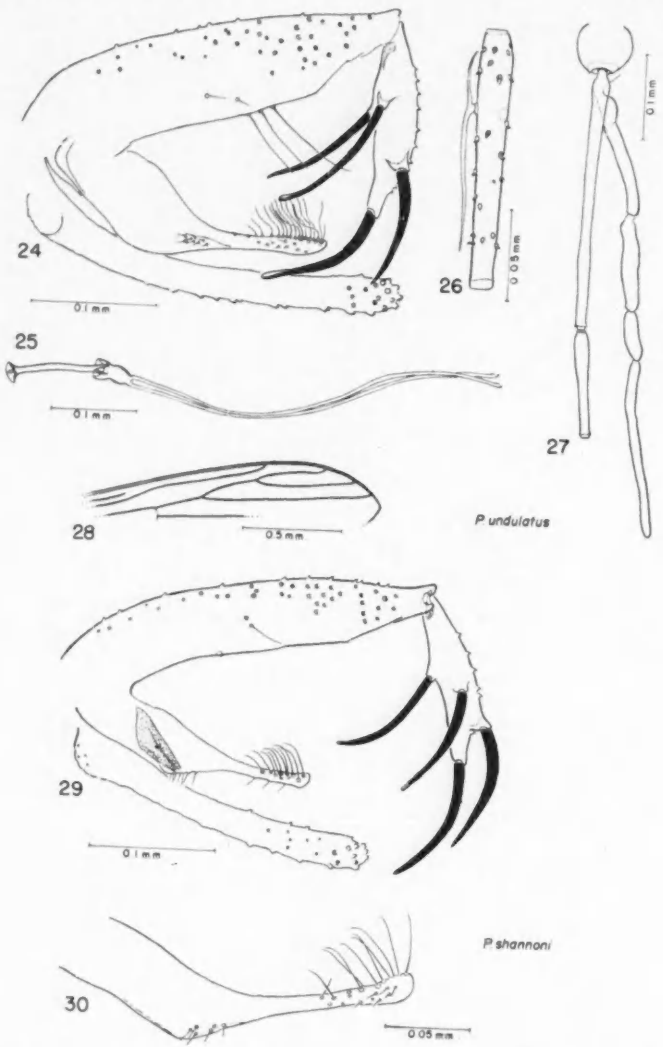
All figures of this and other plates were drawn by the authors with a camera lucida from balsam or copal-phenol-balsam slide mounts, unless otherwise indicated.



P. shannoni. All figures are from females except figs. 14-*a*, *b*. FIG. 7. Posterior end of cibarium, pigmented patch not shown. FIG. 8. Entire cibarium. FIG. 9. Third palpal segment, showing distribution of Newstead's scales. FIG. 10. A group of Newstead's scales enlarged. FIG. 11. Spermathecae, drawn in phenol before treatment with KOH to show outer envelope, which at times, as in this case, surrounds the "head." FIG. 12. Another spermatheca drawn in phenol before KOH treatment. FIG. 13. Same spermathecae as fig. 12, drawn in water after treatment with KOH. FIG. 14. First and second sternites, *a*, *b*, males; *c*, *d*, females.

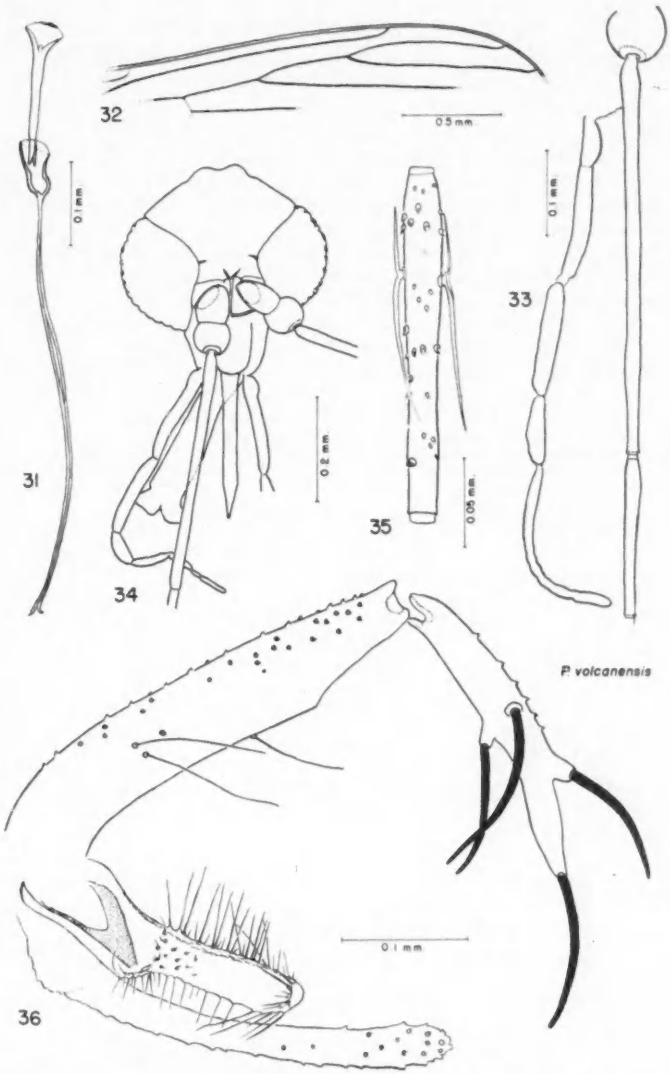


P. punctigeniculatus. Figs. 15–20, males; figs. 21–23, females. FIG. 15. Male genitalia, inner aspect. FIG. 16. Genital filaments and pump. FIG. 17. Antennal segment IV, showing ascoids. FIG. 18. Palp and basal antennal segments. FIG. 19. Wing. FIG. 20. First and second sternites. FIG. 21. Spermatheca, drawn in phenol. FIG. 22. Posterior end of cibarium. FIG. 23. Entire cibarium.



P. undulatus, sp. nov. All figures are of males. FIG. 24. Male genitalia, inner aspect, slide no. 406, holotype. FIG. 25. Genital filaments and pump. FIG. 26. Antennal segment IV, showing ascoids. FIG. 27. Palp and basal antennal segments. FIG. 28. Wing.

P. shannoni. FIG. 29. Male genitalia, inner aspect, of the form with reduced numbers of setae on the parameres. FIG. 30. Paramere of fig. 29 at greater magnification.



P. volcanensis, sp. nov. All figures are of males. FIG. 31. Genital filaments and pump. FIG. 32. Wing. FIG. 33. Palp and basal antennal segments. FIG. 34. Head, dorsal view. FIG. 35. Antennal segment IV, showing ascoids. FIG. 36. Male genitalia, inner aspect, slide no. 652, holotype.

A NEW SPECIES AND SOME RECORDS OF TRIDENCHTHONIID PSEUDOSCORPIONS

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During the past few years, the writer has received a number of collections of pseudoscorpions of the family Tridenchthoniidae (Dithidae). These collections serve as the basis for the present short report. The material examined belongs to and is deposited in four different institutions, as indicated by the following key: AMNH, American Museum of Natural History; CNHM, Chicago Natural History Museum; INHS, Illinois Natural History Survey; and USNM, United States National Museum.

Verrucaditha spinosa (Banks)

1893. *Chthonius spinosus* Banks, Canad. Ent., 25: 67.
1929. *Verrucaditha spinosa* Chamberlin, Ann. Mag. Nat. Hist., (10)4: 59.
1945. *Verrucaditha spinosa* Chamberlin and Chamberlin, Bull. Univ. Utah, 35(23): 24.

RECORDS: One female (CNHM), Evansville, Indiana, H. Dybas, June 28, 1943; one female (INHS), in fungi, Norco, Louisiana, C. L. Remington, Sept. 8, 1944; one male (INHS), at light, Chalmette, Louisiana, C. L. Remington, Oct. 15, 1944; one tritonymph (INHS), under bark, Norco, Louisiana, C. L. Remington, Nov. 3, 1944; one female, one nymph, and one male (INHS), under bark, Norco, Louisiana, C. L. Remington, Nov. 2, 1944; one female (AMNH), Sam A. Baker State Park, Missouri, C. J. Goodnight, Aug. 27, 1941. These records extend the range of this species considerably to the west, the species having previously been found in the Gulf States from Florida to Mississippi and as far north and west as Illinois.

Tridenchthonius mexicanus Chamberlin and Chamberlin

1945. *Tridenchthonius mexicanus* Chamberlin and Chamberlin, Bull. Univ. Utah, 35(23): 57.

RECORD: One female (AMNH), María Andreas, Puebla, Mexico, Goodnight and Bordas, Aug. 24, 1946.

Tridenchthonius serrulatus (Silvestri)

1918. *Chtonius* (sic!) *serrulatus* Silvestri, Boll. Lab. Zool. Gen. e Agrar., Portici, 12: 294.
1945. *Tridenchthonius serrulatus* Chamberlin and Chamberlin, Bull. Univ. Utah, 35(23): 50.

RECORDS: One male and two females (AMNH), Tafo, Gold Coast, Africa, from under bark, R. G. Donald, March 19, 1946, "B104." While the present specimens appear to have palpal podomeres that are a little larger and a little more slender than described for *T. serrulatus* by Chamberlin and Chamberlin (1945), there seems to be no doubt of the proper species determination.

Tridenchthonius addititius, new species

Because of the detailed description of the genus *Tridenchthonius* Balzan as given by Chamberlin and Chamberlin (1945), it seems unnecessary to give more than a brief diagnosis of this new species.

Male.—Description of the male is based on the holotype and one paratype. Each measurement for the paratype is given in parentheses immediately following the corresponding measurement of the holotype. Golden yellow in color; body fairly stout; condition of holotype precludes all possibility of an accurate measurement of the body length; paratype somewhat folded but probably about 1.1 or 1.2 mm. in length. Carapace subquadrate in general outline; anterior margin weakly bilobed, usually with four marginal setae on each lobe; epistome triangular in shape, margin serrate as is the medial portion of the margin of each lobe; posterior margin of carapace definitely concave and with six marginal setae; medial portion of carapace more or less free of setae, total number of setae on carapace about 80; anterior eyes much more highly developed than the posterior eyes; carapace 0.36 (0.38) mm. long, 0.45 (0.45) mm. in greatest width, posterior width of carapace 0.45 (0.44) mm., ocular width 0.37 (0.41) mm. Abdomen as usual in the genus; abdomen of neither specimen in a position suitable for observing the chaetotaxy, but sternites and tergites of middle portion of abdomen appear to have from 10 to 14 setae; abdomen of paratype probably 0.7 to 0.8 mm. long, 0.44 mm. wide.

Chelicera with eight or nine accessory setae, in general resembling closely the chelicera of *T. serrulatus* (Silvestri) as described and pictured by Chamberlin and Chamberlin (1945, fig. 12B); serrula exterior of 15 or 16 ligulate plates; chelicera 0.277 (0.26) mm. long, 0.156 (0.155) mm. wide across the base; movable finger 0.155 (0.153) mm. in length.

Palpus as usual for the genus, appearing much like that of *T. serrulatus* (Silvestri) as described by Chamberlin and Chamberlin (1945); maxilla of holotype 0.24 mm. long, 0.135 mm. wide; trochanter 0.182 (0.182) mm. long, 0.11 (0.097) mm. wide; femur 0.40 (0.405) mm. in length, 0.097 (0.103) mm. wide, length 4.1 (3.95) times the width; tibia 0.205 (0.201) mm. long, 0.10 (0.113) mm. in width; chela 0.58 (0.59) mm. long, 0.12 (0.125) mm. wide, length 4.85 (4.7) times the width; depth of chelal hand subequal to width, 0.116 (0.12) mm., length of hand 0.225 (0.23) mm.; movable finger 0.37 (0.39) mm. in length. Each chelal finger with between 45 and 50 teeth, usually a few more on the fixed finger than on the movable finger.

Legs as usual in the genus. First leg with trochanter 0.117 (0.116) mm. long, 0.093 (0.088) mm. deep; pars basalis 0.233 mm. in length in the holotype, 0.241 mm. long in the paratype, depth 0.058 (0.054) mm.; pars tibialis 0.163 (0.159) mm. long, 0.048 mm. deep in both males; tibia 0.136 (0.144) mm. long, 0.039 (0.043) mm. deep; tarsus of paratype 0.233 mm. long, 0.035 mm. deep. Fourth leg with entire femur 0.365 mm. long in both males, 0.17 (0.167) mm. deep; tibia 0.27 (0.275) mm. long, 0.078 mm. deep in both specimens; metatarsus 0.132 (0.13) mm. long, 0.05 mm. deep in both males; both holotype and paratype with telotarsus 0.26 mm. long, 0.035 (0.036) mm. in depth.

Female.—Description based on the allotype. Female very similar to the male. Body length 1.15 mm.; carapace 0.38 mm. long, 0.405 mm. wide, with ocular breadth 0.40 mm. Chelicera with movable finger 0.133 mm. long, relatively much shorter than in the male; chelicera 0.272 mm. long, 0.155 mm. wide; 15 plates in the serrula exterior. Palpus with maxilla 0.25 mm. long; trochanter 0.185 mm. long, 0.108 mm. wide; femur 0.41 mm. long, 0.105 mm. wide, length 3.9 times the width; tibia 0.233 mm. in length, 0.11 mm. in width; chela 0.61 mm. long, 0.133 mm. wide, length 4.6 times the width; chelal hand 0.225 mm. in length, 0.132 mm. in depth; movable chelal finger 0.39 mm. long. First leg with pars basalis 0.249 mm. long, 0.059 mm. deep; pars tibialis 0.156 mm. in length, 0.050 mm. deep; tibia 0.144 mm. long, 0.043 mm. deep; tarsus 0.241 mm. in length, 0.038 mm. in depth. Fourth leg with trochanter 0.195 mm. long, 0.102 mm. deep; entire femur 0.399 mm. in length, 0.156 mm. in depth; tibia 0.272 mm. long, 0.07 mm. deep; metatarsus 0.140 mm. long, 0.047 mm. deep; telotarsus 0.27 mm. in length, 0.036 mm. in depth.

Tritonymph.—With characteristics common to the tritonymphs of this group; the only data given here being the measurements of the carapace and palpus of the single available paratype. Body length about 0.86 mm.; carapace 0.37 mm. long, 0.325 mm. wide across the posterior margin, ocular breadth 0.255 mm. Palpus with trochanter 0.16 mm. long, 0.095 mm. wide; femur 0.31 mm. long, 0.082 mm. wide; tibia with length of 0.179 mm., width of 0.092 mm.; chela 0.48 mm. long, 0.101 mm. wide; chelal hand 0.195 mm. long, 0.102 mm. deep; movable chela finger 0.295 mm. long.

Type locality.—Tropical West Africa. The holotype male, the allotype female, and a paratype tritonymph (all USNM) from Mount Coffee, St. Thomas Island, Gulf of Guinea, collected during March and April, 1897; one paratype male (AMNH) taken from a log, on April 26, 1946, by R. G. Donald, at Amentia Ashanti, Gold Coast.

Remarks.—The present new species differs from other species in the genus chiefly by the size and length-width ratios of the palpal podomeres and by the chaetotaxy of the carapace. While *T. addititius* very closely resembles *T. serrulatus* (Silvestri, 1918) as redescribed by Chamberlin and Chamberlin (1945), it more nearly approximates the Mexican species with respect to the number of setae on the carapace.

Separation of *T. addititius* from the two other known African species of *Tridenchthonius* may be made by the following key:

1. Carapace with more than 100 setae 2
   Carapace with less than 80 setae ..... **additius,** n. sp.
2. Palpal femur with length 4.6 times the width,
   africanus (Beier, 1931) from Mabira, Tropical East Africa
   Palpal femur with length 4.1 to 4.2 times the width,
   serrulatus (Silvestri, 1918) from Nigeria

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STUDIES ON THE FLIGHT RANGE OF CERTAIN SIMULIIDAE, WITH THE USE OF ANILINE DYE MARKER[1]

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It is commonly accepted that certain species of flies of the family Simuliidae, namely, *Simulium* (*Simulium*) *ochraceum* Walker, *S.* (*S.*) *metallicum* Bellardi, and *S.* (*Lanea*) *callidum* Dyar and Shannon, are the most probable vectors of onchocerciasis in Guatemala and Mexico. Although to the present day this has not been experimentally proven, certain circumstances do substantiate this belief. These are: (1) The established presence of adult flies of at least one of the above species in any given part of the onchocerciasis zone; (2) The fact that these flies habitually bite humans; (3) The concurrence of greatest fly population with greatest exposure on the part of the people infected; and (4) The presence of microfilariae in dissected flies of the onchocerciasis region. (These microfilariae undoubtedly often belong to species of filariids that infect other animals.)

Although blackfly breeding is found on almost all fincas (plantations) where onchocerciasis is endemic, there are some fincas on which large populations of the adult fly are encountered but where breeding is either absent or negligible. It is this finding that stimulated the present study. For example, one such finca, Montequina (Municipality of Atitlán, Sololá, Guatemala), comprising 564 acres, is situated on the Pacific slope, southwest of the volcano Atitlán, at an altitude of 3200 feet. During the months of December and January, 1948, surveys of the blackflies breeding in the streams passing through the finca were made by the writer and no breeding was discovered. The following month the author was requested by the manager of the finca to investigate the plague of blackflies that had been biting the employees to such an extent that many were planning to seek employment elsewhere. On February 24th a visit to the finca showed that flies were in great abundance, especially in the region of the administrative buildings and the nearby dwellings. Many of the people were literally "peppered" with bites, and several had applied bandages to swollen parts of their bodies. The presence of adult flies within the buildings was the rule. In one house, as many as 100 blackflies (mainly *ochraceum*, but with small numbers of *metallicum* and *callidum*) were found resting on the muslin used as window-screening. Within the office of the finca the

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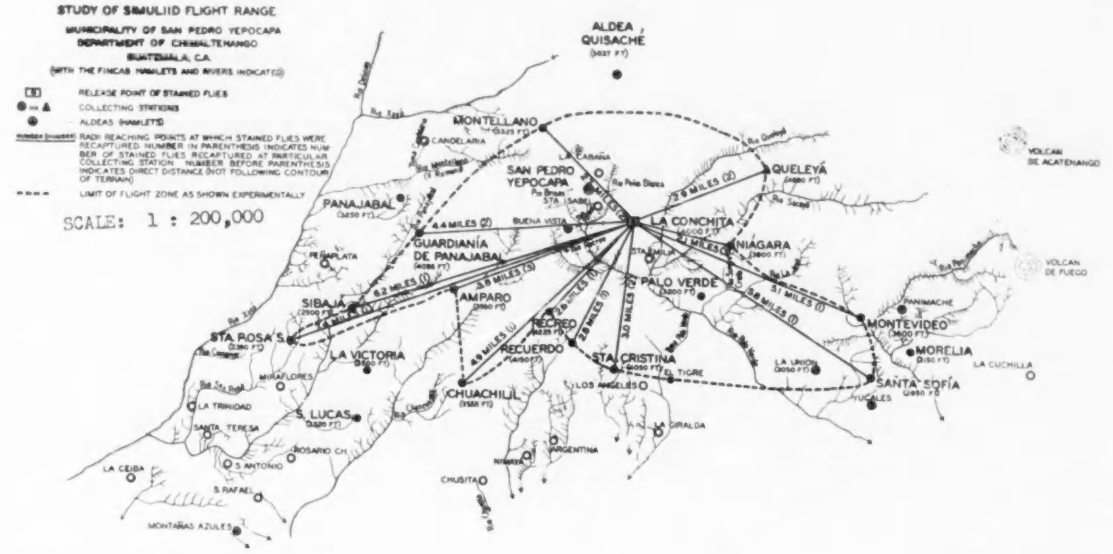
STUDY OF SIMULIID FLIGHT RANGE
MUNICIPALITY OF SAN PEDRO YEPOCAPA
DEPARTMENT OF CHIMALTENANGO
GUATEMALA, C.A.
(WITH THE FINCAS HAMLETS AND RIVERS INDICATED)
RELEASE POINT OF STAINED FLIES
COLLECTING STATIONS
ALDEAS (HAMLETS)
RADII REACHING POINTS AT WHICH STAINED FLIES WERE RECAPTURED. NUMBER IN PARENTHESIS INDICATES NUMBER OF STAINED FLIES RECAPTURED AT PARTICULAR COLLECTING STATION. NUMBER BEFORE PARENTHESIS INDICATES DIRECT DISTANCE (NOT FOLLOWING CONTOURS OF TERRAIN)
LIMIT OF FLIGHT ZONE AS SHOWN EXPERIMENTALLY
SCALE: 1 : 200,000
ALDEA QUISACHE
MONTELLANO
CANDELARIA
SAN PEDRO YEPOCAPA
PANAJABAL
GUARDIANÍA DE PANAJABAL
LA CONCHITA
QUELEYÁ
NIAGARA
PALO VERDE
AMPARO
SIBAJÁ
STA. ROSA S.
LA VICTORIA
RECUERDO
STA. CRISTINA
CHUACHIJIL
S. LUCAS
MONTEVIDEO
MORELIA
SANTA SOFÍA
LA CUCHILLA
VOLCAN DE ACATENANGO
VOLCAN DE FUEGO
MIRAFLORES
LA TRINIDAD
SANTA TERESA
ROSARIO CH.
S. ANTONIO
LA CEIBA
S. RAFAEL
MONTAÑAS AZULES
CHUSITA
ARGENTINA
GIRALDA
LOS ANGELES
EL TIGRE
LA UNIÓN
HUCALES
PANIMACHE
BUENA VISTA
LA CABAÑA
STA. EMILIA
PEÑA PLATA
4.4 MILES (2)
3.8 MILES (3)
3.5 MILES (2)
2.8 MILES (2)
5.1 MILES (1)
4.9 MILES (1)
3.8 MILES (1)

flies seemed to bite as willingly as they did in the fields. This perhaps was due to the many open doors and windows which created a rather diffuse light similar to that outside the building. Comparatively few flies were found in the native huts which were constructed of mud and straw, presumably because of the extreme obscurity within. Outdoors the flies fed voraciously, always preferring situations with diffuse light; in the open sun they always chose the shaded side of the individual. The fly population on Montequina seemed in excess of that usually encountered on fincas in the onchocerciasis zone, but the habits of the flies ran true to form. A thorough survey of the streams flowing through the finca was made during the three days following, but still no breeding was found.

That part of the finca mainly affected is situated on a sharp ridge, with deep, extensive ravines on both sides. The ridge is so narrow that even a small vehicle (jeep) must back out of the area because of the lack of room for executing a turn. Because of the exposure of this ridge to winds from both the Pacific Ocean and the North, it was suspected that the simuliids had perhaps been blown into the region with squalls that had just abated. The closest fly breeding was estimated to be at least three miles from the area in question.

Spraying of all buildings, both inside and outside, with 5 percent DDT in kerosene was suggested and this, with additional spraying of the grounds in the environs, was done within a few days. Almost immediately thereafter the finca became practically blackfly-free. Long after the normal development of several generations of blackflies could have taken place the finca was still without flies. Thus it seemed quite clear that the heavy populations of flies either had been carried by winds to the finca or had migrated to it from neighboring breeding places.

It was not until February, 1949, that the entomological work of the Onchocerciasis Laboratory, situated at San Pedro Yepocapa (Chimaltenango, Guatemala), was considered far enough advanced to allow time for a flight range study. A review of the literature disclosed no records of previous flight range investigations with *Simulium*. In a few papers, mention has been made of the finding of simuliid flies at various distances from the nearest breeding places. Edwards (1) found *Simulium venustum* two miles from its probable source. However, this report was based solely on the collection of adults at a particular area rather than on the recapture of marked specimens which had been released a known distance away. Edwards also failed to mention the prevalence of the winds and the availability of blood meals in the area.

METHODS AND CONDITIONS

In the present study, made in the region of San Pedro Yepocapa, it was found impracticable to follow in their entirety the techniques usually employed. The equipment used for detecting fluorescent dyes would have been difficult to maintain in the field, and preliminary surveys would have been necessary to determine the extent to which field-caught flies were carriers of naturally occurring fluorescent particles and which these were (Reeves et al., 2). Light traps, often employed in flight range and population studies of mosquitoes, would have been

inapplicable since blackflies are normally active only from sunrise to sunset. Even if the traps had been applicable, the necessity of carrying storage batteries or generators for the operation of the traps to and from the field by foot, and the need for constant surveillance of the equipment would have precluded their use. Thus a system using simple methods and easily transportable equipment had to be devised. Since the flies to be marked and recovered were not needed for further experimental work, it was not necessary to keep them alive thereafter. Metallic dusts and aniline dyes were possibilities.

Metallic dusts[2] were tested in the laboratory with wild flies. The necessity for minute, microscopic examination of each individual fly collected, and the difficulty in preventing contamination with the dusts, made their use impractical. Aniline dyes[3] were next tested for their ability to adhere to the flies and the facility with which they could be detected with the aid of solvents.

A modification of the marking and examination techniques used by Clarke (*3*) was employed. Each dye was prepared by grinding it in a mortar with refined wheat flour[4] for one-half hour, in the proportion of one part dye to nine parts flour. The solvent was composed of three parts absolute ethyl alcohol, two parts glycerine, and one part chloroform.

Ten field-caught flies were placed in each of ten 23-ml. test tubes, which were stoppered with cotton. A minute quantity of the particular dye powder being tested was blown into the tubes by means of glass tubing with a rubber bulb. After a ten-minute settling period, the flies were transferred to large, clean glass vessels. The flies were kept segregated according to the dye with which they had been treated, and a part of each group was examined after one, two, and three days. The flies were observed under the dissecting microscope as they were placed, one at a time, in the solvent. Stained flies imparted to the solution the characteristic color of the dye. After several repetitions of this procedure, it was found that a one-minute settling period gave equally as good staining as did a ten-minute period. This method of marking gave good results, with over 90 percent of the treated flies exhibiting stain, and with no greater mortality among the stained flies than among unstained controls. Safranin Bluish was chosen for the subsequent field experiments because of the ease with which it was detected.

The experiments in the field were carried out from February 22nd to May 26th, 1949. The area chosen for the experiments covers approximately 50 square miles in the municipality of San Pedro Yepocapa, situated on the western slope of the volcanoes Acatenango and Fuego, at altitudes 2500 feet to 5500 feet (See map). The terrain is very rough, with wide and deep ravines, high cliffs, and steep

[2]Venus Richgold Brilliant and Venus Palegold Brilliant No. 4, manufactured by the United States Bronze Powder Works, Closter, New Jersey.

[3]Carmine, Victoria Green, Safranin Bluish, Safranin O, and Methylene Blue Chloride, all made by the National Aniline Division of the Allied Chemical and Dye Corp., New York, N. Y.

[4]Chalk was first tried as a carrying agent but it seemed to cause heavy mortality of the flies.

slopes, always subject to heavy erosion by the mountain streams that rapidly pass over them. Almost all land is part of some finca, and the administrative buildings or native habitations of these gigantic plantations dot the area. There are also the small hamlets so typical of Guatemala. Approximately 20 to 35 percent of the land is cultivated to coffee, sugar cane, banana, or corn, while the rest is a dense, temperate to semi-tropical, rain forest. The area experiences two main seasons, the rainy season, usually extending from April through October, and the dry season, which extends from November through March. The flight range experiments here discussed overlapped the two seasons.

During the period February 22nd through March 31st, no rain was recorded; the average maximum and minimum temperatures for the period were 78.6° F. and 61°F., with absolute maximum and minimum temperatures of 86° F. and 55.4° F. respectively; the average relative humidity was 85, with maximum and minimum of 100 and 43. During the period April 1st through May 26th, 33.4 mm. (1.3 inches) of rain fell during 22 days; the average maximum and minimum temperatures for the period were 78.8° F. and 61.5° F., with absolute maximum and minimum temperatures of 84.2° F. and 59° F. respectively; the average relative humidity was 89, with maximum and minimum of 100 and 63. In this region, during a part of the year, October through December, the winds are extremely strong. During these months there is a complete diurnal reversal of wind direction from the north during the morning and from the south during the afternoon. When these experiments were under way, during the hours of greatest fly activity the winds constantly shifted, apparently with no definite pattern.

The municipality of Yepocapa is almost entirely within the zone of endemic onchocerciasis. The three species of flies that were used in the experiments (*S. ochraceum*, *metallicum*, and *callidum*) are all found throughout the experimental area, where there is a normal population of their hosts, both humans and domestic animals, and where breeding places of the flies are abundant. No attempt was made to use laboratory-reared flies for the flight range experiments, since it was not known to what extent laboratory rearing would affect their development and activity.

Each morning, between the hours of 8:00 a. m. and 11:00 a. m., two men made collections of wild flies at the release point, Finca La Conchita (See map). Each used the other as bait. The flies were collected by placing the mouth of a 23 ml. test tube over them as they were feeding. As soon as the tube contained 40 flies, the number of each of the three species (practically the only species biting humans in the region) was noted and the safranin-flour mixture was introduced. By using the same tube for catching and as a dusting chamber, excessive handling was avoided. After one minute, allowed for the particles to settle, the flies were released. The holding time from capture to release never exceeded 15 to 20 minutes. This procedure was continued for the entire three-hour period. During the 94-day period covered by these experiments, stained flies were released on 75 days.

Beginning on the same day as the first release of stained flies, the collection of flies was made at twenty collecting stations located at

places where larvae, pupae, and adult flies had been collected in the past. No attempt was made to use areas of maximum fly-biting or of maximum breeding. Since previous findings at the Finca Montequina and at other localities indicated that the flies travel great distances, collecting stations were established from two to eight miles from the release point. Although they were situated in all directions from La Conchita, the greater number were placed to the south, since to the north and east the terrain is much less accessible and supports a much smaller fly population. Only six collectors were available, and visits to collecting stations had to be made on foot. Since the area containing the fincas San Lucas, La Victoria, Santa Rosa, Sibaja, and Amparo was

TABLE I

COLLECTING STATIONS AND NUMBER OF TIMES EACH WAS VISITED

Finca	Distance from Release Point (miles)	No. of Times Visited	Finca	Distance from Release Point (miles)	No. of Times Visited
Niágara	2.1	57	Panajabal	4.8	61
Palo Verde	2.1	57	La Union	4.8	34
Recreo	2.6	36	Chuachilil	4.9	13
Montellano	2.7	28	Montevideo	5.1	34
Recuerdo	2.8	36	Santa Soffa	5.8	5
Queleyá	2.9	27	Sibajá	6.2	49
Santa Cristina	3.0	36	Morelia	6.3	5
Quisache	3.0	34	La Victoria	6.3	32
Amparo	3.8	56	San Lucas	7.1	15
Guardianía Panajabal	4.4	46	Santa Rosa	7.4	50

TOTAL NUMBER OF COLLECTIONS MADE—711.

too distant to permit making the round trip, including the collection of the flies, in one day, two collectors visited this zone together and remained there over a two-day period. To all other fincas, only one collector was allotted. Even with one-man teams, it was impossible for all collecting stations to be covered every day. It will be seen in Table I how many times each station was visited during the experiments.

RESULTS AND DISCUSSION

From February 22nd to May 21st a total of 19,580 flies were stained and released, of which 9,931 were ***metallicum***, 8,675 ***ochraceum***, and 974 ***callidum***. From February 22nd to May 26th, 711 collections were made at the twenty stations, a total of 18,707 flies being captured.[5]

[5]It will be noted that fewer flies were collected by the six collectors than were stained by the two men at the release point. This discrepancy can be accounted for by considering: (1) that each collector usually had to collect the flies for himself, while the men staining flies were able to use each other as bait; and (2) that the number of stations visited by a collector were many, thereby limiting the time spent at any particular one, while at the release point collections were made continuously over an extended period of time.

Of this number 21 were stained flies. These included 9 ***ochraceum***, 8 ***metallicum***, and 4 ***callidum***. They were recovered at distances ranging from 2.1 miles up to 7.4 miles from the release point. Table II shows the distances at which the flies of each species were recovered. No correlation can be made as the number of flies under consideration is much too small. Table III summarizes by periods, each containing seven days on which releases and collections of flies were made, the total number of flies of each species stained and released, the number of flies collected at the twenty stations, the number of stained flies of each species recovered, and the distance from the release point at which the latter were recaptured.

It is, of course, impossible to determine the actual distances travelled by the recaptured stained flies. Considering the extreme irregularity

TABLE II

RECOVERIES OF STAINED FLIES

FINCA	DISTANCE FROM RELEASE POINT (miles)	NUMBER OF FLIES RECOVERED		
		Simulium ochraceum	*Simulium metallicum*	*Simulium callidum*
Niágara	2.1	2	1	....
Montellano	2.7	1	1	....
Queleyá	2.9	1	1	....
Amparo	3.8	1	2	....
Guardianía Panajabal	4.4	2	....	....
Chuachilil	4.9	1	....	....
Santa Sofía	5.8	1	....	....
Recreo	2.6	....	1	....
Sibajá	6.2	....	1	....
Santa Rosa	7.4	....	1	....
Recuerdo	2.8	....	....	1
Santa Cristina	3.0	....	....	2
Montevideo	5.1	....	....	1
Totals	.....	9	8	4

of the terrain, some of the ravines traversed being over 500 feet deep and over a mile wide, it is quite probable that the distances noted may be more than doubled.

It will be noted in Table III that one stained ***Simulium metallicum*** was recovered 3.8 miles from the release point on February 23rd, the day following the first release of stained flies. This indicates a very rapid flight and the likelihood that the flies travel great distances. Unfortunately, the regularity with which the stained flies were released and the use of only one dye preclude any further estimates of the rapidity of migration of the flies.

Because of the relatively few collecting stations in the large experimental zone, the necessity for confining them within eight miles (calculated as a straight map distance) of the release point, and the

TABLE III

RECORD OF STAINED FLIES RELEASED AND RECOVERED

PERIOD*	NUMBER OF FLIES RELEASED				TOTAL NUMBER OF FLIES COLLECTED	STAINED FLIES RECOVERED		
	ochraceum	*metallicum*	*callidum*	Total		Species	Number	Distance (miles)
22–28 February	375	908	440	1723	1812	*metal.*	1	3.8 (23 Feb.)
1– 7 March	1324	1327	103	2754	3224	.....#	.....	.....
8–15 March	1317	1258	90	2665	2740	*metal.*	1	3.8
16–23 March	1064	1275	59	2398	673	*calli.*	1	2.8
24–31 March	602	1550	86	2238	3166	*ochra.*	1	4.9
						calli.	1	3.0
1– 8 April	726	1084	59	1869	2403	*ochra.*	1	3.8
						ochra.	1	4.4
						metal.	1	2.6
						metal.	1	6.2
						calli.	1	3.0
9–20 April	1071	784	46	1901	873	*ochra.*	1	5.8
						ochra.	1	2.9
						ochra.	1	2.1
21–28 April	933	603	30	1566	1080	.....#	.....	.....
29 April–6 May	516	466	27	1009	903	*ochra.*	1	2.7
						ochra.	1	4.4
7–14 May	409	430	9	848	1006	.....#	.....	.....
16–23 May	338	246	25	609	766	*ochra.*	1	2.1
						calli.	1	5.1
						metal.	1	7.4
24–26 May	0	0	0	0	361	*metal.*	1	2.1
						metal.	1	2.7
						metal.	1	2.9
Totals	8,675	9,931	974	19,580	18,707	.....	21	.....

*During each period listed releases and collections were made on only seven days. The last period comprises only three days.
#No stained flies were recovered during this period.

irregularity of collections at them, it cannot be considered that the maximum range of flight has been determined. However, this was not the prime purpose of the experiment. It was desired, rather, to discover if the capacity of flight of the blackflies was such that they could migrate from a zone in which onchocerciasis is endemic to one that is supposedly free of the disease, there propagate their kind, and perhaps introduce and maintain the disease.[6] This is of extreme importance in Guatemala where the zones of onchocerciasis are considered to be rather circumscribed. Assuming that *S. ochraceum*, *metallicum*, and *callidum* are the vectors of onchocerciasis in Guatemala, the capacity of these species for making long-distance flights makes possible the extension of the disease beyond its present boundaries, should environmental conditions in neighboring areas be as suitable for fly-breeding as they appear to be.

SUMMARY

This paper presents the first published experimental data on the flight range of the Simuliidae.

The aniline dye, Safranin Bluish, has proved very efficient for marking wild-caught adult simuliids in these studies. The use of a solvent, composed of absolute alcohol, glycerine, and chloroform, greatly facilitated the recognition of the dye on recaptured flies. Details are given of the method found most satisfactory for the application of the dye.

The flight range of the blackflies was shown to be at least 7.4 miles. Because of the small number of stained flies recaptured, no attempt was made to correlate the flight capacity of the three species under consideration.

A flight of 3.8 miles in one day was recorded for one female.

The apparent similarity of environmental conditions affecting blackfly development between the onchocerciasis zones and the surrounding areas, and the great flight capacity of the probable vectors of the disease, are highly important facts to be taken into account in any consideration of the possible spread of onchocerciasis beyond its present confines.

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[6] "The Effective Flight Range" of Russell *et al.* (4).

ON DICRANOSTOMUS, A REMARKABLE PERUVIAN GENUS OF KATYDIDS; AND NOTES ON OTHER INSECTS HAVING ELONGATE MANDIBLES

(Orthoptera: Tettigoniidae)

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This report has two main objectives: First, to contribute information on the distribution and taxonomic characters of the katydid genus *Dicranostomus* Dohrn; second, to acquaint general entomologists and teachers with the principal features of these very unusual South American insects. The most conspicuous feature of these katydids is a pair of forceps-like appendages borne on the anterior surfaces of the mandibles. Most North American entomologists are scarcely acquainted with such structures except in males of the dobsonfly, *Corydalus* Latr. (Megaloptera). For this reason I have assembled brief notes on representative cases of striking mandibular structures that occur among mandibulate insects of other orders, mentioning examples that have come to my attention through the kindness of several colleagues.

Only three specimens of *Dicranostomus* are known, one of them being the male illustrated (Pl. I), which is the only example I have seen. It is from the humid forests of eastern Peru, where it was taken at Fundo Sinchono, Department of Huanuco, at an elevation of about 5,000 feet, by the professional collector Jose Schunke, August 5, 1947. Mr. Schunke, who is fully aware of the unusual nature of this insect, writes me that he has seen no other specimen in many months of collecting.

There have been two basic contributions on the genus *Dicranostomus*, Heinrich Dohrn in 1888 (Stettin Ent. Ztg. 49: 361–362, pl. 2, figs. 2a, 2b) and Brunner von Wattenwyl in 1895 (Monog. Pseudophylliden, Vienna, pp. 19, 179–180, fig. 83). Dohrn named the genus[1] and described one species, ***monocerus***, based on a female from the Peruvian locality Cumbasi, near Huallaga, a District in the Department of San Martin, and about 180 miles northwest of Tingo Maria in the Huallaga Valley. In his monograph of pseudophylline katydids, Brunner indicated the position of the genus and described a second species, ***nitidus***, based on a male from Peru (no detailed locality given).

The size of both of the earlier recorded specimens is essentially like the present one. The pronotum of ***monocerus*** was described as granulose, that of ***nitidus*** as smooth, the latter condition being true of my example. The female of ***monocerus*** had mandibular appendages approximately as long as the pronotum. In Brunner's male of ***nitidus*** they were nearly twice as long as the pronotum, while in mine the

[1]The name "*Dicranostomus*" is derived from two Greek words, meaning "pitchfork" and "mouth."

appendages are slightly more than two and one-half times as long as the pronotum. Because of our limited knowledge regarding secondary sexual characters, as well as of the characters distinguishing species in this genus, it seems advisable to identify my specimen as ***Dicranostomus nitidus*** Brunner. In view of the great rarity of preserved specimens known to exist, it is hoped that the descriptive notes here furnished will be helpful to future students. Obviously, more material is needed to show the limits of species, what variation exists, and how the sexes differ in addition to genitalic and tegminal characters.

The present specimen of *D. nitidus* is 58 mm. in overall length,[2] approximately one-third of that measurement being represented by the mandibular appendages. Another noteworthy feature of this genus is the sharply tapering, curved horn, that arises from the front of the head, between the eyes. Each mandible bears a single appendage on its anterior, external surface. The appendage is broadly and strongly attached, with no suggestion of being shed at any time during the insect's life. Except for the appendages, the mandibles are not unusual, bearing several well-formed teeth on the opposed chewing surfaces. In this respect these mandibles differ markedly from those of *Corydalus*, the latter not being used for chewing and the long forceps-like structures themselves constituting the main structures of the mandibles, not merely appendages of mandibles. The mandibular appendages of *Dicranostomus* curve forward and are shaped as illustrated (figs. 1 and 2).[3] No trace of segmentation is evident, though each appendage has irregular transverse ripples that reflect the light. The points are very sharp.

Nothing is known concerning the function, if any, of these appendages. Certainly they must move considerably during the routine chewing of food, but because of the manner of attachment the apices apparently do not separate and close in the way they would if the arms swung from a single fulcrum. Four possible functions could be suggested, but for none of them is there any evidence in this case: First, grasping the opposite sex during mating; second, defensive use when attacked; third, holding prey in the event that other insects are eaten; fourth, attacking others of the same sex at mating time. Both sexes have at least short mandibular appendages, so the situation is not entirely comparable to that exemplified by various lucanid beetles, the males of which have specialized mandibles to use in combat whereas the females have simple mandibles. In the complete absence of information on the habits of *Dicranostomus*, or on the nature of its food, there is just as much reason to suspect that these appendages developed as a product of orthogenesis, with no useful function at the present stage of their evolution.

Notes on habitat.—Fundo Sinchono, where the illustrated specimen was collected, was established during the recent war as an experimental cinchona plantation. It is at an elevation of about 5,000 feet on the eastern slope of the Cordillera Azul, just over the ridge from the Huallaga Valley and about 37 miles east of Tingo Maria on the road to Pucallpa.

[2]More formal descriptive notes are grouped near the end of this paper.

[3]I am greatly indebted to H. C. Wilcox, of the U. S. Department of Agriculture, or the photographs.

The Cordillera is the last important range of the Peruvian Andes at this latitude (about 80° 30′ S.) before reaching the lowland pampas of the Amazon basin. Rain is plentiful, about 125 inches annually, and well distributed so that rain forest is the rule. Wild species of *Cinchona* are among the dominant forest plants.[4] The specimen of *Dicranostomus* was found at the edge of a little depression in the jungle, where there was an accumulation of matted dead leaves on the ground and conditions were dark and humid.

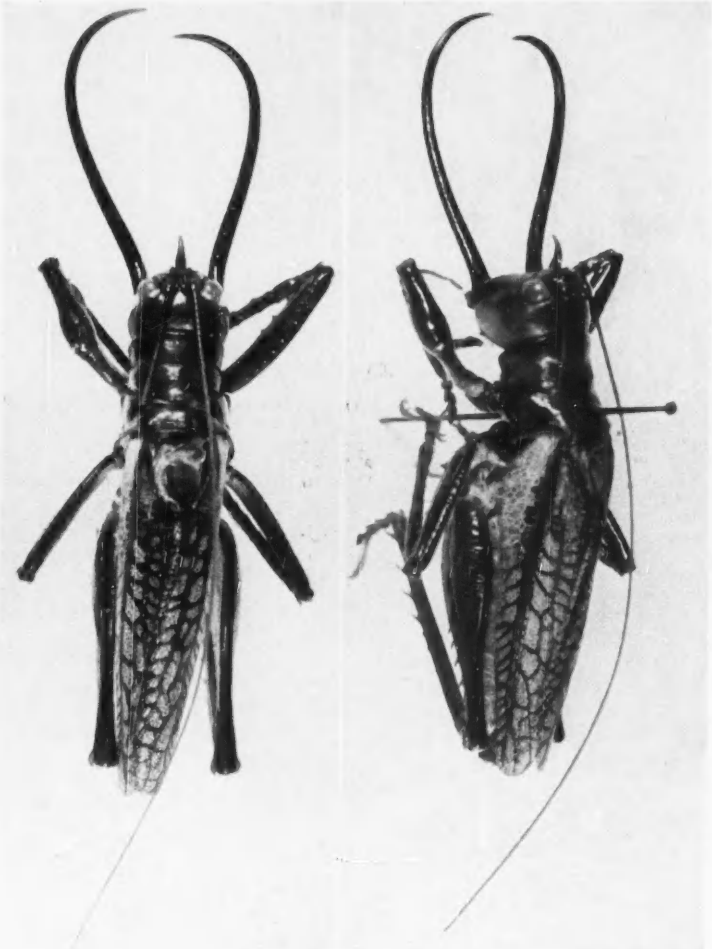
Taxonomic notes.—*Dicranostomus* belongs to the Group Cocconoti of the subfamily Pseudophyllinae. The basic generic identification key is that of Brunner (*l. c.*), now long out of date. Lawrence Bruner (1915, Ann. Carnegie Mus. 9: 336–345) presented a key to Neotropical genera of Pseudophyllinae, closely adapted from that of Brunner. It should be noted that in the first couplet of Brunner's key (*l. c.*, pp. 9, 13) the word "mesosternum" should be substituted for "mesonotum," the latter being an error. In Brunner's diagnosis of the genus (*l. c.*, p. 179), *Dicranostomus* is said to have four spines on the hind femur, and to have a genicular spine present only on the internal lobe of the middle femur. On the other hand, Brunner's figure of *D. nitidus* plainly shows six spines on the ventral margin of the hind femur, and the same number occur in my specimen. The latter has a distinct genicular spine on the internal (or posterior) lobe of both middle and hind femora, and there is a strong possibility that the genicular spine of the hind femur was overlooked in Brunner's specimen.

In the following summary of characters noted for the Fundo Sinchono specimen, which is deposited in the U. S. National Museum, generic and specific features cannot be satisfactorily segregated in all cases; therefore, the two have been combined in view of the brief descriptions now available for both the genus and the two species.[5]

Male (Fundo Sinchono, Peru).—Head largely smooth and moderately polished; lower part of face inconspicuously, transversely wrinkled; antennae well separated; basal antennal segment unarmed, a broadly rounded elongate ridge on lower face; fastigium narrowly but strongly sulcate, the apex somewhat elevated, extending forward to about middle of antennal scrobes; a frontal spine arising between antennal scrobes, curved, tapering and acute; eyes slightly higher than long, essentially as in *Cocconotus*, mandible with strong frontal appendage as illustrated. Pronotum smooth, with sparse short pile, moderately shiny, anterior margin smooth; no trace of lateral carinae; disk of metazona directed dorsoposteriorly at about a 45° angle with disk of prozona; principal sulcus strong, extending nearly whole width of lateral lobes, prozona with much more shallow minor sulcus not extending onto lateral lobes;

[4]My friend W. H. Hodge, of the University of Massachusetts, has kindly sent me notes on the character of this area; in fact, Dr. Hodge personally assisted in establishing the plantation. For photographs of the village of Fundo Sinchono and of representative jungle scenes nearby, as well as a discussion of the main botanical features, readers are referred to Hodge (1948, Economic Botany 2: 229–257, 34 figs.); also to "Hunting Cinchona in the Peruvian Andes," by the same author (1944, Jour. N. Y. Bot. Gard. 45: 32–43, 18 figs.).

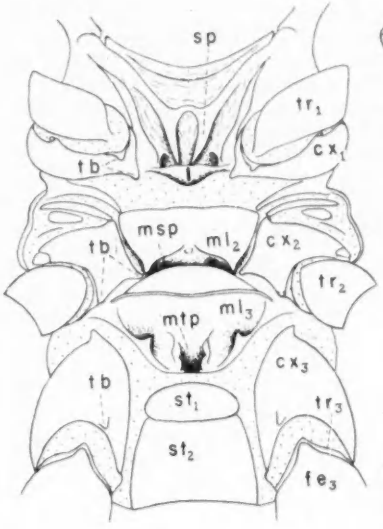
[5]Rehn's diagnosis of *Polyancistrus* (1936, Trans. Amer. Ent. Soc. 62: 274) suggests the type of characters which usually prove to be of generic importance in this group of Orthoptera.



Dicranostomus nitidus Brunner, male. Fig. 1. Dorsal view. Fig. 2. Latero-dorsal view. (Length from tip of mandibular appendage to tip of wing, 58 mm.) Photograph by H. C. Wilcox.

ABBREVIATIONS

as—antennal scrobe
ce—compound eye
cer—cercus
cx_1, cx_2, cx_3—coxa of front, middle and hind leg
fe_3—femur of hind leg
fs—frontal spine
ml_2—mesosternal lobe
ml_3—metasternal lobe
msp—mesosternal pit
mt—mesal tooth of cercus
mtp—metasternal pit
sa—supra-anal plate
sg—subgenital plate
sp—prosternal spine
st_1, st_2—first and second abdominal sterna
sy—stylus
tb—tubercle of coxa
tr_1, tr_2, tr_3—trochanter of front, middle and hind leg.



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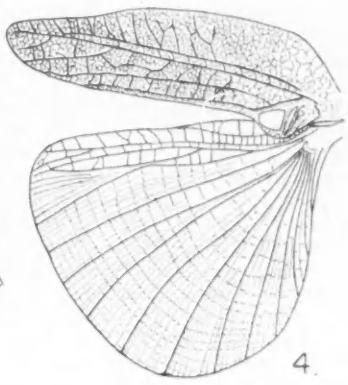

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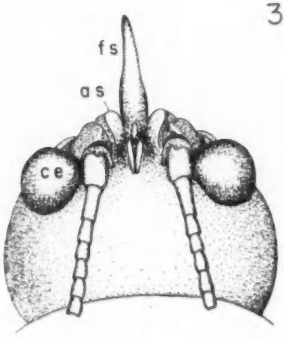

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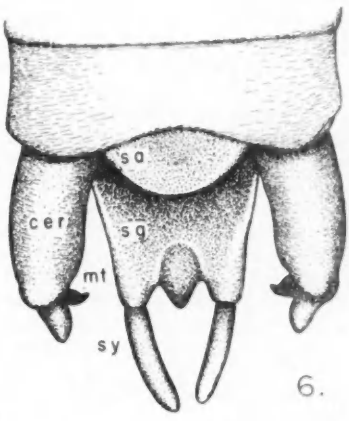

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Dicranostomus nitidus Brunner, male. Fig. 3. Ventral view of thorax and base of abdomen, somewhat diagrammatic. Fig. 4. Left tegmen and wing. (Length of tegmen, 26 mm.) Fig. 5. Dorsal view of head, mandibular appendages not shown. Fig. 6. Dorsal view of apical portion of abdomen (magnification twice that of fig. 5).

(Drawings by the author)

tegmina and wings as illustrated, curving about abdomen in repose. Paired prosternal spines (fig. 3, *sp*) long, acute, extending nearly to the level of apices of front coxae; prosternal pits separated slightly more than tips of spines, a shallow longitudinal groove behind a ridge that closes pits posteriorly; mesosternal pits (*msp*) moderately separated, shallow, inconspicuous; mesosternal lobes (ml_2) acutely triangular, the posterior points directed sharply ventroposteriorly; metasternal pits (*mtp*) a single longitudinal, deep groove; lobes less triangularly produced than mesosternal ones, directed nearly ventrally, so that observer examining specimen in ventral view looks almost directly onto apices of lobes. Front coxae with rather long, acicular, triangular spine from anterior face (not shown in fig. 3); front and middle coxae have two blunt tubercles (*tb*) on mesal margin; hind coxae has single ventral tubercle near apex.

Front femur with four spines in apical five-eighths of ventral front margin (left femur abnormally swollen near middle, apparently due to an injury); front tibia with seven pairs of small ventral spurs, more widely spaced basally, larger apically, front dorsal margin with five low rounded tubercles; hearing organs of equal length, linear, opening dorsally, closed laterally, the lateral margins on same level with associated dorsal surface of tibia; middle femur with acute posterior genicular spine, four spines on front ventral margin; middle tibia with seven pairs of ventral spurs, dorsoposterior margin with three (left leg) or four (right leg) tiny spurs; hind femur with small posterior genicular spine, front ventral margin with six small curved spines on apical third.

Supra-anal plate broadly, evenly rounded, a ventral apical margin (not seen in fig. 6) giving a triangular appearance when seen in dorsoposterior view, a shallow median depression near base; cercus cylindrical, tapering slightly to specialized apical part, consisting of an inconspicuous dorsal swelling or "boss," a blunt arm extending ventromesally, and a dark, heavily sclerotized mesal tooth (*ml*); subgenital plate with ventral surface of disk broadly inflated, apically with a triangular median tooth; dorsally, a broad, elongate depression at base of median tooth; styli slender, cylindrical, slightly curved; all external genitalia sparsely covered with fine setae (omitted from fig 6) which in length average about the diameter of a stylus, occasional setae much longer.

Coloration: Head, thorax and legs chestnut, the tibiae darker, the mandibular appendages practically black, palpi pale; lower part of face blackish; mandibular face ventrad of appendage very reddish chestnut, teeth of chewing surface jet black; abdomen pale straw colored; tegmen with veins brown, cellules and membrane yellowish, much brighter toward base in costal area; wing with veins pale brown, membrane slightly fuscous.

Measurements (length in millimeters): Overall (tip of mandibular appendage to apex of closed wing), 58; body (base of fastigial horn to apex of cercus), 35; left mandibular appendage, 20; pronotum, 7.5; front femur, 12; front tibia, 13; hind femur, 19; hind tibia, 19; tegmen, 26. Greatest breadth of pronotum, 7.5 mm.; of tegmen, 7.5 mm.

Notes on the mandibles of other insects.—No other Orthoptera with

mandibular appendages comparable to those of *Dicranostomus* have come to my attention, though several genera have elongate mandibles. Particularly in certain South African and Australian Gryllacrididae,[6] greatly elongate mandibles occur, but in most of these examples the main body of the mandible is simply enlarged and ventrally produced, with teeth situated at the end.

Among other mandibulate insects, the elongate mandibular appendages of various beetles are probably best known, aside from the long mandibles of *Corydalus* males already mentioned. Certain Scarabaeidae and Lucanidae are especially worthy of mention. In males of the East Indian scarabaeid genus *Fruhstorferia* the cutting edge is retained near the base of the mandible, while the remainder is greatly prolonged.[7] Many genera of Lucanidae show remarkable mandibular modifications. Species of the South American genera *Chiasognathus* and *Sphenognathus* are among the most striking,[8] with one or two long tapering appendages extending forward from the mandibles of males. I have seen several species of these genera from Chile and Ecuador; so some probably live in the very region where *Dicranostomus* is found. Occasional Cerambycidae are characterized by mandibular appendages, the males of *Dendrobias virens* Casey, which occurs in the southwestern United States, being noteworthy. Long ago, Kirby (1826, Zool. Jour. 2: 70, pl. 1, fig. 7) briefly described a pair of horned mandibles, which had been found in New Zealand on a string of beads in the possession of natives. Each mandible had a long curved arm extending beyond the chewing surface. Kirby suggested that the mandibles might be those of a lucanid or cerambycid. Among the Curculionidae, the majority of broad-beaked weevils emerge from pupae with a deciduous appendage borne on the mandible. This appendage is normally shed early in adult life, leaving a scar which in some cases constitutes an important taxonomic character. These deciduous appendages are briefly discussed by Marshall (1916, Coleoptera, Curculionidae, *in* Fauna Brit. India, pp. 6–8). The male of *Ozognathus cornutus* (Lec.), an anobiid beetle inhabiting the western United States, has a single appendage borne on the anterior surface of each mandible. The appendage is usually directed upward, and it is incurved near the apex. At least one related western species of *Ozognathus* has comparable mandibular horns. But for their small size, these species would probably be better known than at present for these distinctive appendages.

The male of the African wasp, *Synagris cornuta* (L.), has a curved process from the anterior surface of each mandible, which approaches that of *Dicranostomus* as closely as that of any insect that I have seen.[9]

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[6]See Karny, 1937, Orthoptera, Gryllacrididae, *in* Gen. Insectorum, fasc. 206, pl. 1–7, and Tillyard, 1926, Insects of Australia and New Zealand, p. 96. *Hemiandrus monstrosus* of North Auckland (Stenopelmatinae), recently described by Salmon, 1950 (Dominion Mus. Records Ent., N. Z. 1(8): 175, fig. 65) has a horn-like outgrowth extending forward from the base of each mandible, apparently much like the appendages of *Dicranostomus*, though shorter.

[7]Ohaus, 1934, Gen. Insectorum, fasc. 199, pl. 3, figs. 10, 10a.

[8]Jeannel, fig. 100, *in* Traité de Zoologie, Paris, vol. 9 (Insects), 1949.

[9]See Bequaert, 1918, Vespidae of the Belgian Congo, Bull. Amer. Mus. Nat. Hist. 39: 205, pl. 2.

Several genera of ants have very elongate or sickle-shaped mandibles, but I know of none with appendages comparable to those of *Dicranostomus*. The Asiatic genus *Harpegnathus*, illustrated by Wheeler (1926, Ants, p. 17), and the New World genus *Odontomachus*, described and figured by Smith (1947, Amer. Midland Nat. 37: 538), are outstanding with respect to the size and form of their mandibles. In most, if not all, species of the mayfly family Ephemeridae the nymph regularly bears a tusk on the external face of the mandible.[10]

Only a few of the more outstanding examples of specialized mandibular development are mentioned in the foregoing notes, given primarily to indicate the diversity of structures and the wide separation of including orders and families. The mandibles of males of *Corydalus* superficially resemble the mandibular appendages of *Dicranostomus* most closely, but morphologically the structures are not so comparable. Isolated genera of several orders have appendages that are largely comparable, morphologically, though the resemblance is fairly strong in only rare instances, such as the wasp, *Synagris*. In each example mentioned the structures noted probably developed entirely indedendently of those in other groups. Information on extinct and undescribed forms and the functions of their mandibles is essential for a full understanding of these specializations. Though in most groups such data are poorly known or unassembled, with their gathering a marvelous story for the evolutionist would almost surely unfold.

[10]See Needham, Traver and Hsu, 1935, The Biology of Mayflies, pp. 190, 239.

THE LEPIDOPTERISTS' SOCIETY

Word has been received from Frederick H. Rindge, Secretary, of the organization of the Lepidopterists' Society, with a constitution, by-laws, and a full set of officers. The latter include Dr. J. H. McDunnough as President, Mr. A. H. Clark as Senior Vice President, Dr. Rindge as Secretary, and Mr. J. B. Ziegler as Treasurer. The first annual meeting is scheduled at the American Museum of Natural History, New York, December 29 and 30, 1950.

STUDIES ON PROTEOLYTIC DIGESTION IN ADULT AEDES AEGYPTI MOSQUITOES[1]

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INTRODUCTION

The importance of mosquitoes in the transmission of malaria, yellow fever, dengue, encephalitis, and filariasis is well known. Since the etiological agents of all these diseases, protozoans, viruses, and nematode worms, as well as the bacteria and fungi often harbored by mosquitoes, are ingested by the insects before transmission can occur, they are obviously concerned with the digestive systems of their hosts. Extensive physiological investigations of the culicid digestive system may be expected to provide fundamental bearing on the relationships which mosquitoes have with these several disease-producing agents. Data from such research would not only add to the store of our knowledge but might conceivably be utilized in several practical ways also, such as: (a) devising a means of interrupting the development of the micro-organism or virus within the mosquito, thus breaking the transmission cycle[2]; (b) repelling or destroying the mosquito itself as a result of better understanding its feeding and digestive processes[3]; or (c) assisting in the development of procedures for culturing these agents outside the mosquito.[4]

The studies reported here are confined to problems associated with the enzymatic digestion of blood by adult mosquitoes. Inasmuch as the conditions of pH, temperature, time, and state of oxidation under which an enzyme normally functions in the intact living organism are considered, as a general rule, to be close to the conditions of optimum activity for that enzyme it seemed desirable first to evaluate these factors with regard to the test species, *Aedes aegypti*. Approximate values for the average time and temperature of blood digestion in this species are available from the literature. Determinations of pH and of the apparent oxidation-reduction potential of the midgut and crop are a part of the present investigation.

Although digestive enzyme studies have been reported for a number of insects, beginning with Basch (1859) and Plateau (1875), reports on adult mosquitoes are conspicuous by their absence. DeBoissezon (1930)

[1]The studies reported here were done at the University of Minnesota and are included in a Thesis submitted by the author to the Faculty of the Graduate School, University of Minnesota, in partial satisfaction of the requirements for the degree of Doctor of Philosophy.

[2]Whitman (1948) showed that the addition of the anti-malarial drug, M2279, to the artificial blood meal of *Aedes aegpyti* at the same time, or within a few hours of the time that an infective dose of *Plasmodium gallinaceum* (bird malaria) was given, resulted in the destruction of the *Plasmodium*.

[3]DeMeillon and Goldberg (1947) have explored this possibility with the bed bug and a tick, but without success.

[4]Ball (1946) describes *in vitro* culture techniques for *Plasmodium knowlesi*.

followed the digestion of a blood meal in *Culex pipiens* by histological and histochemical methods (although no direct enzyme tests were involved) and Wigglesworth (1943) noted the complete digestion of blood, in the metabolic sense, in *Anopheles maculipennis* and *Aedes aegypti*. Metcalf (1945) was unable to demonstrate the presence of any digestive enzymes in the salivary glands of *Anopheles quadrimaculatus* although he did find a strong agglutinin and anti-coagluin in those organs. The presence of digestive enzymes in mosquito larvae was first demonstrated by Hinman (1933), who also showed that the larvae could ingest and assimilate completely dissolved nutrients from their aquatic medium.

The meagerness of data on adult mosquitoes may not be entirely fortuitous since the small size of these insects necessitates the use of large numbers per test or of greatly increasing the sensitivity and precision of the techniques employed. In the course of this investigation over 3,100 adults were dissected for examination or test.

METHODS

The yellow fever mosquito, *Aedes aegypti* (L.), was the species chosen for the experimental work because of its availability, ease of rearing and handling, and public health importance. *Anopheles quadrimaculatus* Say, the malaria mosquito[5], was also employed for certain tests, but, unless otherwise noted, all data refer to *Aedes aegypti*.

It was found that the midguts or stomachs of newly emerged adults contained a dark green mass of contaminated food debris remaining from larval life. Thirteen agar slants inoculated with midgut contents from these young adults all developed two or more types of bacterial colonies. This mass was egested during the second day following emergence so that by the third day the intestinal tract appeared to be free of bacteria or other debris. Out of 19 agar slants inoculated from 3-day-old mosquitoes, 17 developed one or more bacterial colonies, indicating that, although the midguts of the older mosquitoes appeared to be free from contamination, they were rarely so. As a result of these findings, as well as those of other workers (Bishop and Gilchrist, 1946), who found that *Aedes aegypti* females take blood most readily between the third and fifth days following emergence, mosquitoes within this age range were used exclusively. They were offered 5% sucrose on the first day, then water only, until ready for use. By the third day no food remained in the fore- and midguts and the mosquitoes are referred to as mature, unfed adults.

Hydrogen ion (pH) or oxidation-reduction (redox) potential determinations were made colorimetrically. The appropriate dyes[6, 7] were

[5]Adults of this species were reared from eggs supplied by the Public Health Service, National Institutes of Health, Malaria Investigations Laboratory at Memphis, Tennessee.

[6]The colorimetric pH indicators used, with their respective effective pH ranges are as follows: bromphenol blue (3.0–4.6), chlorophenol red (5.1–6.7), bromcresol purple (5.2–6.8), bromthymol blue (6.5–7.5), phenol red (6.8–8.0).

[7]The oxidation-reduction indicator dyes used, with their respective standard equilibrium potentials, are as follows: sodium 2,6-dichloro-benzenone indophenol (+0.217 volts), thionine or Lauth's Violet (+0.063 volts), methylene blue (+0.011 volts).

either injected directly into the freshly dissected viscera in isolated saline droplets or they were offered in 2.5% sucrose solution on cotton pledgets to the live mosquitoes. After the dyes had been ingested, the mosquotoes were dissected to reveal the color of the ingested dye in the alimentary tract. The feeding technique avoided the difficulties of micro-injection and was preferable for unfed mosquitoes, but unsuited for bloodfed females. Approximate determinations of the midgut pH of blood-fed females were made either by injecting the dye into the blood-filled midguts isolated under oil droplets or by offering the dye mixed with fresh rabbit blood serum and noting the color of the midgut as revealed by subsequent dissection.

Analyses of the gas bubbles recovered from the crops and midguts of adult mosquitoes were made with a Berg Microanalyzer. The bubbles were collected by dissecting a series of adults in a drop of saturated lithium chloride under the flared tip of a capillary tube supported diagonally over the drop and in contact with it. After a sufficient amount of gas (0.2 cubic millimeter or more) had been accumulated, the resulting larger bubble was transferred to the microanalyzer and the gas analyzed as described by Berg (1946). Saturated lithium chloride was also used in the collecting tube and the microanalyzer because of the very low rate of diffusion of gases through that fluid.

Blood-fed females were secured by placing the bare forearm across the top of the lamp chimney in which they were confined. They were allowed only a partial blood meal before being aspirated off into individual vials in which they remained alive for one to two hours before dissection. All other materials offered as food to the mosquitoes were held in cotton pledgets placed on the top netting of the lamp chimneys. An inverted glass funnel surrounded by a cylinder of warm water was used to cover the pledget if the material was to be offered warm.

All glassware used to hold enzyme or substrate material was cleaned by soaking overnight in concentrated nitric acid, rinsed several times in tap water, then four times in distilled water and usually oven-dried. Other glassware was washed in a commercial trisodium phosphate washing powder and rinsed in tap, then distilled water. Except for the cleaning operations just described, distilled water was used wherever water is indicated.

The method of proteolytic enzyme assay developed made use of dissected-out, homogenized midguts or other organs as the enzyme material, heparinized whole rabbit blood as the subtrate, a buffer, and a preservative. Incubation was usually for six hours at 40° C. The intact midguts were dissected out from mature *Aedes* females well in advance of the experiments, accumulated into lots of 25 each, and stored in the deep freezer until needed. Just prior to an experiment they were homogenized, without abrasive, in saline to which sufficient *Merthiolate* preservative[8] had been added to give an ultimate dilution of 1 : 12,500. Two-tenths ml. portions of the resulting brei were then measured into the incubation tubes. At this point the tubes designated as blanks were placed in a boiling water bath for five minutes and then cooled.

[8] *Merthiolate* is the brand name for sodium ethylmercurisalicylate, Eli Lilly & Co., Indianapolis, Ind.

Otherwise the blanks were handled identically with the runs. Next, 0.06 ml. of the substrate, fresh whole rabbit blood to which heparin[9] had been added to inhibit coagulation, was added to all the tubes. In determining the optimum pH of the enzyme the blood was replaced by an approximately 1% solution of serum albumin. The buffers employed were MacIlvaine's citric acid-disodium phosphate (Lange, 1946) or Michaelis' (1931) acetate-veronal buffer added in 0.1 ml. portions. The contents of the tubes were then stirred and incubation begun.

Enzyme activity was measured by increases in free amino nitrogen (incubated runs, less boiled, incubated blanks) as determined by Folin's sodium beta naphthoquinone-4-sulfonate colorimetric procedure as revised by Frame *et al.* (1943).[10] An Aminco Type F (photoelectric photometer was used to determine the optical densities of the final solutions. The technique was checked by using commercial trypsin[11] as the enzyme source.

RESULTS

A number of pH determinations on the digestive systems of insects have been published (Wigglesworth, 1938). In most cases the digestive juices are either weakly acid or weakly alkaline. However lepidopterous larvae, regardless of the type of food taken, always exhibit strongly alkaline reactions (pH 9–10). A few insect species, from other orders, in which microsymbionts or fermentation play a role in digestion show rather acid conditions, *e. g.*, termites with pH 5.2, cockroaches feeding on sugars with 4.4–4.8.

Determinations on blood-sucking insects are less numerous. Kadletz and Kusmina (1929) found an *Anopheles maculipennis* mosquito's midgut to be acid to ingested litmus while the crop was basic. MacGregor (1931) using culicine mosquitoes confirmed their results. He fed a neutral solution of sucrose and found the crop contents, after feeding, to be alkaline (approximately pH 8.5) with B. D. H. Universal Indicator. He also fed a neutral solution of bacto-peptone and found one-half hour later that the stomach was acid (approximately pH 3–4). DeBoissezon (1930) found the pH of the midgut of *Culex pipiens* to be 6–7 during digestion (his method not indicated). Lester and Lloyd (1928) working with the tsetse fly, *Glossina*, found an emulsion of midgut tissues of these insects to have a pH of 6.5. They used neutral red, a dye with an effective range of pH 6.8–8.0, so it is difficult to see how they arrived at their conclusion.

Wigglesworth (1929), also working with *Glossina*, wished to determine the pH of stomach and crop following a blood meal, but found that the color of the blood interfered with colorimetric determination. He therefore fed the flies through a membrane (vulture's skin) with either sheep serum or plasma diluted with saline. Following ingestion of either mixture he got essentially the same results. The midguts

[9]The heparin used was "Liquaemin 100 mg./10 ml.," Roche-Organon Co., Nutley, N. J.

[10]See also Hawk, Oser, and Summerson (1947) for a description of the improved Folin technique.

[11]The commercial trypsin powder used was "Difco Trypsin 1:250," Difco Laboratories, Detroit, Mich.

averaged pH 6.6 and the crops pH 7.3. He also obtained for the more posterior sections of the midgut "where digestion was further advanced" single droplet estimations of pH 6.2 and 6.4.

The results of pH determinations made on the alimentary tracts of mature, unfed adults of both *Aedes aegypti* and *Anopheles quadrimaculatus* are given below. When the indicator dyes were offered with sucrose it was noted that the resulting pH of the crop was often slightly more acid than with the same dyes injected. The effect may have resulted from the 2.5% sucrose present, for the crops of mosquitoes fed on 5% or stronger sucrose always exhibit a definitely acid reaction (pH 5.5). The pH of the midguts as determined by either technique was the same. Although individual variations were evident, the results secured point to the following average pH values for adults without a blood meal:

Estimations of the pH of the stomach after a blood meal were made on *Aedes* females only and there with difficulty. The dye had to be observed where it was not obscured by the ingested blood. The mosquitoes were allowed to take only a small volume of blood and the

	Crop	Midgut		Rectum
		Cardia	Stomach	
Aedes aegypti males or females	5.5–6.0	6.5	6.5	5.8–6.0
Anopheles quad. males or females	"	5.5–6.0	"	"

dissected midgut was isolated in mineral oil. Diffusion of the injected dye away from the stomach was restricted by the oil and its fate could be followed in the wall of the stomach as well as in the limited clear areas in the lumen surrounding the blood mass. With this technique the pH of the lumen appeared to be the same as that of the blood contained, i.e., about 7.3. Apparently the buffering capacity of the midgut compared to that of vertebrate blood is insignificant. It should be noted that the cells of the stomach wall remained slightly acid (pH 6.5), indicating that the buffering effect of the vertebrate blood meal was, as one would expect, limited to the lumen of the gut.

Another set of pH determinations was carried out on *Aedes* females which had been fed 1 : 1 or 2 : 1 mixtures of fresh rabbit serum and a pH indicator solution made saline with added sodium chloride. The mixtures were offered on cotton pledgets rather than through a membrane as Wigglesworth (1929) had done. The midguts of serum-fed females were definitely basic to bromcresol purple and remained so (in the living mosquitoes) for at least 3.5 hours. They were within the range of bromthymol blue. The emerald color noted for this dye in the midguts was a lighter shade (more acid) than the same dye mixed with a pH 7.0 buffer. When phenol red was employed, the rose color observed was darker (more alkaline) than the same dye at pH 7.0. The results with the latter two dyes may be interpreted to correspond to

pH values of 6.7 and 7.3, respectively. The reason for their divergence is not apparent. Twenty-four hours after feeding on the serum: bromthymol blue mixture the mosquitoes showed a color corresponding to about pH 6.4, while those fed serum: phenol red showed approximately pH 6.8.

In comparing the results just reported with those of previous workers on related insects a lack of agreement is apparent. Kadletz and Kusmina (1929) and MacGregor (1931) working with mosquitoes found the midguts to be acid and the crops alkaline. The alkalinity of the crops is particularly surprising, since the present writer found them to be more acid than the midguts. In MacGregor's experiments the crops contained ingested sugar solutions, a situation which in the present investigation led to increased acidity. Wigglesworth (1928) likewise found increased acidity in the intestines of cockroaches following the ingestion of sugar by those insects.

The results of Wigglesworth (1929) with the tsetse fly are scarcely comparably to those from mosquitoes. Tsetse flies are exclusively blood-suckers in which the crop functions simply as a storage receptacle for blood and does not denature or digest the blood in any way. The pH of 7.3 for this organ reflects the pH of the serum fed, while the more acid pH's noted for the stomach indicates that serum breakdown had already begun. As noted by Scheer (1948) and others the chief buffering capacity of whole blood resides in the corpuscles, so that it is possible that if whole blood, instead of serum, could have been used in the experiments of Wigglesworth, an alkaline reaction might also have been noted initially in the stomach of *Glossina*.

Linderstrom-Lang and Duspiva (1936) demonstrated the necessity of a strongly negative oxidation-reduction potential in enabling the larva of the webbing clothes moth, *Tineola biselliella*, to digest wool fibers. They were unable to demonstrate digestion by the isolated midgut tissues until air was excluded and reducing substances added. By feeding wool dyed with redox indicator dyes they established the fact that a redox potential of −0.3 volts at pH 9.5 existed in the caterpillar's midgut during digestion.

Achard and Reiss (1942) have measured the redox potentials of the body fluids of several insects and at various stages in the life cycles of certain of them. These authors (Reiss and Achard, 1943) believe that the intracellular proteases of the silkworm, *Bombyx mori*, synthesize proteins at redox potentials more positive than +0.25 volts and hydrolyze them at less positive, or more negative, potentials. They found that although hydrolysis began at potentials just under +0.25 volts, it was maximum at −0.25 to −0.3 volts. They attempted to correlate the observed potentials in the silkworm with the type of metabolism before and during pupation, *e. g.*, the conditions favoring protein hydrolysis were prevalent while larval tissues were breaking down, while the conditions of synthesis prevailed during the formation of adult tissues. Although the experimental data did not support their hypothesis very strongly, they felt that the hypothesis should not be discarded.

Feeding and injection experiments with mature, unfed *Aedes* females using redox indicator dyes showed no evidence of reduction of any of

the dyes, except in the instance detailed below. No bleaching of the dye was observed, neither could the dye color be intensified by concontinued exposure to air or to oxidizing agents. Then sodium 2,6-dichlorobenzenone indophenol was retested with isolated midguts and crops, using a small paraffin cell from which oxygen was removed and excluded by a stream of nitrogen. Under these conditions the fluid-filled crops of dye-fed mosquitoes remained unbleached for over an hour. Because little or no dye had entered the midguts of this same batch of mosquitoes, it was necessary to inject the dye. When the injected midguts were then exposed to nitrogen the color gradually bleached until they were completely colorless in half an hour. After air was again admitted to the cell the blue color of the dye returned to full intensity within a minute. The reduction of the redox indicator by the stomach tissues under these conditions may have been occasioned by the injury to the tissues by the injection process.

TABLE I

RESULTS OF ANALYSES OF GASEOUS SAMPLES USING THE BERG MICROANALYZER

Source of Sample	Air	CO_2 (impure)	12 *Aedes*, both Sexes	15 *Aedes*, Males
Initial volume of sample in cubic millimeters	2.3	4.9	0.19	0.71
Percent carbon dioxide	none	92.0	none	0.8
Percent oxygen	19.5	none	11.8	11.4
Percent nitrogen	80.5	8.0	88.2	87.8

Additional information on the state of oxidation of the digestive tract was afforded by analyses of gas bubbles obtained from the crops and midguts of *Aedes* adults. According to Marshall and Staley (1932) these bubbles first appear while the mosquito is emerging from the pupa as a result of air swallowed by the adult to aid in its release from the pupal skin. The air first enters the stomach, but later is passed forward through the proventriculus to lodge in the diverticula, dorsal and ventral (the ventral diverticulum being the crop). The volume of the air bubbles may vary through the life of the mosquito and their location may alternate between the stomach and the diverticula, but Marshall and Staley found them to be absent only in hibernating females. Other authors agree as to the presence of the bubbles, but disagree as to their mode of origin or replenishment, some claiming them to be the result of anaerobic fermentation processes.

Accumulations of gas bubbles from two series of adults are listed in Table I and indicate about 88% nitrogen, 12% oxygen, and less than 1% carbon dioxide, a decrease of approximately 40% in the amount of oxygen as compared with atmospheric air. The first group of adults had not been fed for over two days, while the second group was tested more than three hours after feeding. Equilibrium conditions relative to gaseous interchange were therefore assumed to exist.

The near universal presence of gas bubbles in the mosquitoes would, by virtue of the oxygen shown to be present, establish an oxidation-reduction potential of +0.8 volts[12] in the fluid contents of crop and midgut. It should be noted, however, that these bubbles are generally more numerous in the diverticula than the stomach, especially after a blood meal when the stomach is distended with fluid. It is possible that under these conditions a greatly reduced oxygen tension may occur in the midgut, corresponding to that experimentally produced when the injected midguts were held under nitrogen.

Taken together, the results of the colorimetric tests and the analyses of the gas bubbles indicate that a negative redox potential is seldom, if ever, possible in the alimentary tract of mosquitoes and that it is evidently not essential for protein digestion, as is the case with the clothes moth larva.

The gas analyses further indicate that the gas bubbles present in mosquitoes are derived from aspirated air. The presence of oxygen and near absence of carbon dioxide in the bubbles rules out the possibility of anaerobic fermentation. The simplicity of the Berg analysis technique for very small gas samples commends it for future use in insect physiological studies, such as analyses of the contents of air sacs or large tracheae.

Determinations of the amino nitrogen content of whole mosquitoes were made at various intervals up to 24 hours following a blood meal in order to follow, if possible, changes in total amino nitrogen content as a consequence of digestion. It was anticipated that the results might approximate those from an ***in vitro*** enzyme test, except that the incubation of substrate with enzyme would be carried out in the living insects. The approximation would have been closer had the contents of each midgut been separated from the rest of the mosquito before analysis so that changes within the midgut might have been contrasted with shifts in amino nitrogen elsewhere in the body.

Combined results of determinations on three batches of *Aedes* females are summarized in Table II. Since the samples were weighed before the amino-nitrogen analysis it is possible to express the results in mg. amino nitrogen per gram of mosquito. It will be noted that although the freshly engorged females more than doubled their average weight in the process of feeding, the concentration of amino nitrogen in these individuals dropped to less than half. The drop was due to the amino-nitrogen concentration of the ingested rabbit blood being only about one-tenth that of the unfed mosquito's haemolymph. The diluting effect of the vertebrate blood on the concentration of amino nitrogen in the insect can be eliminated by expressing all concentrations in terms of initial body weight of the mosquito, as is done in the last column of Table II. Expressed in this manner, no increase in amino nitrogen is apparent during the first three hours following feeding, but from then on the concentration increases at an apparently uniform rate through the final determination at 24 hours.

[12]The equilibrium potential of the theoretical oxygen electrode at one atmosphere pressure and pH 7 is close to 0.8 volts (Bull, 1943). Reducing the oxygen tension to 0.1 atmosphere (10% O_2) would depress the potential less than 0.01 volt (Clark, 1928).

Since the rate of increase in amino nitrogen has been expressed in a quantitative manner it is of interest to calculate this rate in terms of digestive activity, i. e., mg. amino acids released/mg. midgut tissues/hour. The rate thus obtained can then be compared with the results of the enzyme tests and with the estimated enzyme activity of a hypothetical living mosquito. The rate of digestive activity is expressed per given weight of midgut tissues, since, as will be demonstrated later, these are the tissues which secrete the proteolytic enzymes. In order to do this the midguts had to be accurately weighed in the moist state or measured. The latter operation was chosen. A group of eight *Aedes* females, weighing an average of 1.2 mg. each, were dissected and their intact midguts measured with an ocular filar micrometer both as to total volume and thickness of stomach wall at various points. Cal-

TABLE II

SUMMARIZED RESULTS OF AMINO-NITROGEN DETERMINATIONS MADE ON INTACT *Aedes aegypti* MOSQUITOES BEFORE AND FOLLOWING BLOOD MEALS

Type of Mosquito	Tests Included	Number of Adults	Total Wt. in mg.	Av. Wt. in mg.	Total μg. N/ Sample	mg. N/ gm. Mosq.	mg. N/ gm. Initial Wt. of Mosq.
Unfed adults....	*b, c*	30	40.8	1.4	52.0	1.3	1.3
Freshly engorged	*a, b, c*	27	79.3	2.9	43.6	0.6	1.2
3 hours later.....	*b*	10	18.6	1.9	16.0	0.9	1.2
6 hours later.....	*a, b*	28	55.8	2.0	53.9	1.0	1.4
12 hours later.....	*b, c*	17	30.9	1.8	43.2	1.4	1.8
24 hours later.....	*c*	10	20.1	2.0	36.6	1.8	2.6

culations from these measurements gave 0.03 cubic millimeters as the average volume and 0.03 mg. as the average weight of midgut tissue per female.

The weight of amino acids released is derived from the observed increase in free amino nitrogen by assuming the protein substrate to contain 16% total nitrogen of which 80% is free amino nitrogen. On this basis the uniform rate of increase in amino nitrogen noted above corresponds to 0.0208 mg. amino acids released/mg. midgut tissue/hour.

By making several reasonable assumptions[13] it is estimated that a normal living *Aedes* female completely digests a blood meal in 72 hours, which corresponds to an average rate of 0.11 mg. amino acids released/mg. midgut tissue/hour—considerably higher than the uniform rate of net increase in the amino nitrogen of live mosquitoes just noted.

[13]Total hydrolysis of the blood proteins, which amount to 20% by weight of the whole blood is assumed. A full blood meal equals the weight of the unfed mosquito.

The results of the enzyme tests using blood as a substrate are summarized in Table III. The last item in the table, commercial trypsin, was included as a check on the technique. Except for the dissection and freezing, the trypsin preparation was carried through the same procedures as the mosquito tissues in the other tests. When the activity of the commercial trypsin is expressed in quantitative terms it becomes 0.025 mg. amino acids released/mg. trypsin powder/hour.

Reference to Table III will show that of all the tests using blood as a subtrate only one series, the second, showed significant enzyme activity, i.e., the average net amino nitrogen recovered (run less blank)

TABLE III

SUMMARY OF ENZYME TESTS WITH FEMALE *Aedes aegypti*; RABBIT BLOOD SUBSTRATE

Enzyme Source	Total Number of Tests	Total Number of Runs	Average Difference (runs less blanks) in μg. Amino Nitrogen	Greatest Variation within any Test in μg. Amino Nitrogen
1. Midguts dissected from unfed mosquitoes	7	11	+0.4	±0.7
2. Midguts from blood-fed mosquitoes	7	13	+4.0	±0.7
3. Midguts from 5% sucrose-fed mosquitoes	2	8	+0.5	±0.6
4. Midguts + crops from unfed mosquitoes	3	6	−0.9	±0.7
5. Midguts + salivary glands from unfed mosquitoes	2	4	+0.9	±0.1
6. Midguts + salivary glands + crops from unfed mosquitoes	1	2	+0.9	±0.4
(7. 0.16 mg. commercial trypsin powder per run)	1	4	+3.1	±0.9

NOTE: Runs comprised enzyme brei plus heparinized rabbit blood as substrate plus buffer and were incubated six hours at 40° C. Blanks used boiled enzyme brei; otherwise identical.

was greatly in excess of the maximum variation between tests. In this series the midguts were from mosquitoes which had been allowed to take a partial blood meal before dissection. Since the blood-fed mosquitoes used for this series were otherwise similar to those used in the first series, all of which resulted in an insignificant degree of enzyme activity, it is apparent that in *Aedes aegypti* there is an increase in the amount or activation of the proteolytic enzymes following a blood meal. Such a secretion of digestive enzymes in connection with feeding is well known among mammals where it is stimulated not only by the presence of food in the digestive tract or by the normal peristaltic muscular contractions of the tract but also by such nervous stimuli as the sight,

odor, or even thought of food. Among insects such responses have been recorded only by Schlottke[14] (1937a, b), and, accordingly, it seemed desirable to examine the nature of this response in more detail.

Perhaps the process of feeding is in itself the necessary stimulus to protease secretion. To determine whether the response would follow the act of feeding on a substance other than blood, adult females were allowed to feed to repletion on 5% sucrose. In so doing they performed practically the same ingestion cycle as if they were sucking blood, except that the sucrose solution went to the crop instead of the stomach. No increased enzyme activity in the midguts from this series was noted.

The remaining series of experiments were designed to test the hypothesis that some accessory factor necessary to stimulate the secretion of, or to activate, the protease in the midgut is produced elsewhere in the misquito and is passed into the stomach with the blood during feeding. The hypothecated factor might be a coenzyme, a kinase, or a simple organic or inorganic activator, and it might be formed in the salivary glands or the crop. Or the reaction might be involved in the trypsin-antitrypsin complex which Schmitz (1937) has shown exists in human blood. In this case the "activator" might act as an inhibitor or neutralizer of the blood antitrypsin. The method of test was simply to incubate together (with substrate) (a) midguts (from unfed mosquitoes) plus crops, (b) midguts plus salivary glands, and (c) midguts plus both crops and salivary glands. Positive results were not secured from any of these combinations. In fact, the combination of midguts plus crops resulted in lower recoveries of amino nitrogen from the runs than from the blanks, although the differences were not great enough to be significant.

Had positive results been secured with any of the combinations, the added organs would have been tested alone to ascertain whether or not the organ in question might be supplying the complete enzyme, rather than an aceessory factor.

Although Schlottke[14] (1937a, b) appears to be the only investigator to have reported for insects a stimulated secretion of proteolytic enzymes in response to feeding, others have reported cyclical changes in pH and in the histological picture presumed to represent secretory activity of midgut epithelium following a meal. Schlottke worked first with other arthropods. He failed to get a stimulatory response after feeding the horseshoe crab, ***Limulus***, but with a spider he did observe some increase in activity. His best data, however, were from insects—a predacious ground beetle, ***Carabus auratus***, and an omnivorous pygmy grasshopper, ***Tettigonia cantans***. With both insects, the sharpest increase in trypsin occurred within the first hour after feeding. It was clearly evident in the first half hour and remained at a high level for several hours. In the tests reported here the blood-fed mosquitoes remained alive for an hour or more after feeding. Judging from Schlottke's data it is likely that the mosquitoes had exhibited the maximum increase in protease secretion before they were dissected.

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[14]The recent paper by Day and Powning (1949) provides additional data on the stimulation of enzyme secretions following feeding. A hormonal, rather than neural, stimulus is favored.

Expressed on a quantitative basis the most favorable *in vitro* test with blood as the substrate—utilizing midguts from blood-fed mosquitoes—exhibited an average rate of 0.019 mg. amino acids released/mg. midgut tissue/hour. In this same test only 0.34% of the available substrate in each incubation tube was hydrolyzed during the six hour incubation period. It seems clear from the amount of hydrolysis just calculated, that even 0.06 ml. of substrate per tube was in excess of that needed to stabilize the enzyme and to assure maximum opportunity for its activity. This emphasizes the importance of the midgut: substrate ratio. Whereas a large *Aedes* female will not take over two mg. of blood at a feeding, the amount of blood per midgut in the enzyme tests was usually greater than four mg. A possible situation which might account for the low rate of digestion under these conditions (of low midgut: substrate ratio) would be the interference of the mosquito protease by the trypsin-antitrypsin complex of Schmitz (1937) already referred to. If some of the mosquito protease were required to neutralize the blood antitrypsin, then the more blood present, the more *Aedes* protease would be used up in this manner.

Another factor contributing to the relative inefficiency of the *in vitro* tests is that the amount of enzyme material available for the test is limited to that initially present, less losses due to denaturation and manipulation, whereas in the living mosquito the amount of enzyme is increased or sustained by the secretion of additional amounts of enzyme from time to time.

The physical nature of the blood may also be a factor. Blood for the enzyme tests was treated with heparin to prevent coagulation during handling and a true coagulum never formed, although some settling occurred. Metcalf (1945) found ingested blood in the stomachs of *Aedes aegypti* to be coagulated, and in *Anopheles* to be agglutinated. The physical state of the blood mass in the living mosquito is therefore different than in our tests. The possible significance of this difference will be discussed later.

Preliminary experiments designed to determine the optimum pH of midgut protease were unsuccessful. When the buffered incubation mixtures were checked with a Beckman glass electrode pH Meter, Model G, it was found that the buffer then in use, Michaelis' acetate-veronal, was totally inadequate to shift the mixture more than one pH unit. This was due to the high buffering capacity of the vertebrate blood which completely eclipsed that of the Michaelis buffer at the concentrations employed. MacIlvaine's citric acid-disodium phosphate buffer at triple the recommended concentration was able to shift measured quantities of blood to the desired pH values but did not maintain the values initially secured. It was eventually decided to abandon blood as the substrate for this series in favor of serum albumin, since incubation mixtures of the latter were readily adjusted to and maintained at the desired pH values by MacIlvaine's buffer.

The results of this series are plotted in Figure 1. Reference to the figure will show that the data of the three tests, in so far as they overlap, all point to the same region of optimum activity, namely about pH 7.8, a typical value for trypsin. The observed pH optimum for the protease derived from the midguts of blood-fed *Aedes*, acting on serum albumin

substrate, is close to the normal pH of mammalian blood[15] and to that of the blood-filled midguts, but not to the pH of the midguts of unfed *Aedes* adults, which is about 6.5.

The 1% serum albumin proved to be a suitable substitute for whole blood, in fact it supported a 2.75 times higher rate of enzyme activity, 0.052 mg. amino acids released/mg. midgut tissue/hour (at pH 8), than was reached by the most favorable blood substrate test.

In view of the fact that in all insects for which a proteolytic enzyme has been experimentally confirmed, trypsin, not pepsin, has been the protease found[16], the statement of Sumner and Somers (1947) is of

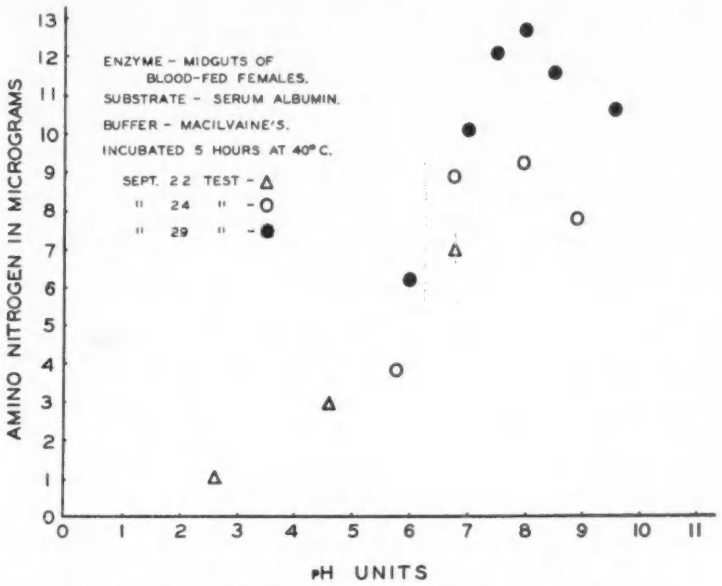
ENZYME - MIDGUTS OF BLOOD-FED FEMALES.
SUBSTRATE - SERUM ALBUMIN.
BUFFER - MACILVAINE'S.
INCUBATED 5 HOURS AT 40° C.
SEPT. 22 TEST - Δ
" 24 " - O
" 29 " - ●
AMINO NITROGEN IN MICROGRAMS
0 1 2 3 4 5 6 7 8 9 10 11 12 13
pH UNITS
0 1 2 3 4 5 6 7 8 9 10 11

FIG. 1. Influence of pH on the activity of *Aedes aegypti* protease.

interest: "Trypsin catalyzes the hydrolysis of peptide linkages in proteins and partly hydrolyzed proteins. Unlike pepsin, it is not an enzyme of first attack and, in several instances, it possesses only feeble action upon native proteins. It does not, for example, readily digest collagen, ovalbumin, serum globulins and hemoglobin. These proteins are readily digested by trypsin once they have been denatured by heat or any other means."

If the trypsins of insects conform to the statement above it follows

[15]Human blood has a pH of 7.3-7.4. Rabbit blood was found to be pH 7.8 with the Beckman pH Meter.

[16]Dipeptidases have also been occasionally noted (Wigglesworth, 1928), but pepsins are still unrecorded for invertebrate animals.

that the insects must either have some means of denaturing any native proteins upon which they feed or be relatively inefficient in the digestion of those proteins. In the case of mosquitoes it is possible that the coagulation or agglutination of the ingested blood serves to denature it sufficiently for digestion to begin. That the ultimate digestion of blood by mosquitoes is quite complete has already been pointed out. By contrast, some other insects, notably lice and fleas, digest blood relatively incompletely (Wigglesworth, 1943).

In mammals trypsin is not secreted in the active state, but rather as the precursor or zymogen, trypsinogen, which is converted to trypsin by enterokinase. No such zymogen: kinase relationship has been noted for insects, except the observation by Schlottke (1937a) that hog enterokinase would increase the activity of trypsin from *Carabus*. He could not locate any enterokinase in the beetle, however. Not only enterokinase, but trypsin itself, activates trypsinogen, so that an initially small amount of trypsin can cause the release of larger and larger amounts of active enzyme from a supply of the zymogen. The previously mentioned data from living *Aedes* females (in which the observed total amino nitrogen content did not increase substantially during the first three hours after a blood meal, but was followed by a uniform rate of increase from the third past the twenty-fourth hour) are suggestive of the possibility that an autocatalytic increase in trypsin from secreted trypsinogen was occurring during those first few hours.

Returning to the optimum pH determination we find that the results secured for *Aedes aegypti* agree closely with the optima secured for the tsetse fly and the cockroach by Wigglesworth (1929). Wigglesworth compared his pH curves for these two unrelated insects with the curve he secured for mammalian pancreatic trypsin. He found that the curves for the two insects could be superimposed and both were more active in the acid range (pH 5–7) than mammalian trypsin. When the date for *Aedes* are replotted in such a manner as to be compared with Wigglesworth's figure it is noted that they fall about midway between his mammalian and insectan curves so that no conclusions can be drawn from the comparison. The curve derived by Schlottke (1937a) for *Carabus* trypsin is also similar to that for *Aedes* except that he found a rather broad optimum zone between pH 8 and 9.

The similarity of the pH optima for insect trypsins is closer than the reported pH's of the midguts for the same insects. Wigglesworth found the pH of the serum-filled tsetse fly stomach to be about 6.6 and that of the cockroach on a protein diet to be 6.3. The midgut of blood-fed *Aedes*, as estimated by the writer, is about 7.3–7.8 depending on the blood contained. Yet all three of these insects have a trypsin of the same pH optimum—pH 7.8. Yonge (1937), Scheer (1948), and others have stated that the pH of the digestive organs of all animals are generally at or near the pH optima of the particular digestive enzymes involved. In this respect the *Aedes* mosquito appears to illustrate this generalization better than either of the insects tested by Wigglesworth.

It has long been known for mosquitoes that ingested blood passes directly to the stomach while other fluids, such as nectar or water, pass first to the crop and dorsal diverticula. Several hypotheses regarding this "switching mechanism" have been advanced but the fundamental nature of the mechanism remains obscure. DeBoissezon (1930) stated

that the small diameter, three microns, of the ducts leading to the crop and dorsal diverticula prevented the entrance of erythrocytes into these organs. His measurements were made on fixed tissue sections and did not take into account the flexibility of the living material. To test his contention several *Aedes* adults were offered a mixture of honey and defibrinated chicken blood,[17] which contains nucleated erythrocytes measuring about 8 by 13 microns. On subsequent dissection it was found that in all those mosquitoes which ingested the mixture both the honey and the blood, including erythrocytes, had entered the crop. Reference has already been made to the gas bubbles which are present in both midgut and diverticula and may pass from one to the others. These would not pass through openings of three microns diameter except under considerable pressure. A more plausible suggestion (Marshall and Staley, 1932) is that the relaxation of the proventricular valve or sphincter to allow blood to enter the stomach at the same time closes the openings into the three diverticula since these openings are immediately adjacent to the sphincter. This explanation does not, however, indicate the nature of the stimulus involved.

It has been suggested (MacGregor, 1931) that feeding from droplets, called "discontinuous suction," results in the crop being filled, while feeding through a membrane, called "capillary penetration," fills the midgut. Later studies (Bishop and Gilchrist, 1946) have demonstrated that it is the nature of the food, not the method of feeding, which determines its destination, *e. g.*, blood taken through a membrane or from a droplet passes to the stomach, while sugar solution taken by either method goes to the diverticula.

Feeding experiments were undertaken by the writer to discover, if possible, some relatively simple property or properties of blood which enable it to pass directly to the midgut, but the results were negative in every test. That is, the mixtures offered were found, by subsequent dissection, to have entered the crop and diverticula in greater amounts than the midgut, or were scarcely ingested at all. The blood properties simulated were: pH, temperature, peptone content, amino acid content, viscosity, osmotic pressure, and the particulate nature of the erythrocytes. They were tested singly or in certain simple conbinations, but in no case did they approach the complexity of whole blood.

SUMMARY

1. Preliminary to the proteolytic enzyme studies the pH of the alimentary canal was determined. Indicator dye solutions were either fed the adult mosquitoes or injected into the dissected-out viscera. In both sexes of *Aedes aegypti* and *Anopheles quadrimaculatus* individual variations were noted, but average values of pH 6.5 for the midgut and pH 5.5–6.0 for the crop and dorsal diverticula were secured. In *Aedes* females following a blood meal the pH of the lumen of the stomach approached that of the blood contained, *i. e.*, pH 7.3, while the crop, which contained no blood, remained acid. This shift in midgut pH is thought to be due to the high buffering capacity of the vertebrate blood.

[17]Bishop and Gilchrist (1946) found that although whole blood, corpuscles, blood plasma and blood serum went directly to the stomach, mixtures of blood and honey passed to the crop.

When fresh rabbit serum plus indicator dye was offered to *Aedes* females the pH of the midgut was found to lie between 6.7 and 7.3 and to shift in the acid direction with time.

2. Feeding and injection experiments with oxidation-reduction indicator dyes gave no evidence of reduction except when isolated midguts were held in a cell under nitrogen gas for half an hour.

3. Microanalyses of the gas bubbles recovered from midguts and crops showed them to contain about 12% oxygen and less than 1% carbon dioxide. This confirmed published statements that they are derived from air bubbles swallowed from time to time during feeding. So long as air bubbles are present and contain oxygen the redox potential of the midgut and crop must be close to +0.8 volts. These data, together with the results just cited, support the view that a low, or negative, redox potential is neither normal nor essential for digestion in these insects.

4. Using the same amino-nitrogen determination procedure employed in the enzyme tests, the total amino-nitrogen content of whole mosquitoes was secured. No increase in amino nitrogen was noted for three hours following a blood meal, but from then on a uniform rate of increase prevailed for at least 24 hours.

5. The method of proteolytic enzyme assay devised utilized dissected-out, homogenized midguts or other organs as the enzyme material, heparinized whole rabbit blood as the substrate, and a buffer. Enzyme activity was measured by increases in free amino nitrogen determined colorimetrically.

It was found that the protease activity of midguts dissected from mature, unfed *Aedes* females was insignificant, while the activity of midguts from females permitted a partial blood meal one to two hours prior to dissection was significant. Attempts to stimulate a significant degree of enzyme activity by using midguts from sucrose-fed females, or by the addition of equal numbers of salivary glands or crops or both to the midguts from unfed mosquitoes were all unsuccessful. It is apparent that the presence of blood in the stomach stimulates proteolytic activity, but that neither the feeding syndrome in itself, nor the replete, distended abdomen, nor a mixing of precursors and activators from different regions of the digestive system, nor an enzyme origin other than the midgut is responsible for this stimulation. Nervous intermediation is conceivable but at present it can only be concluded that for unknown reasons proteolytic activity was not found except following a blood meal.[18]

6. In determining the optimum pH of the *Aedes* protease it was found preferable to use 1% serum albumin as the substrate in place of blood. A fairly sharp optimum near pH 7.8 was secured, a typical value for trypsin.

7. By making several reasonable assumptions it is estimated that a normal living *Aedes aegypti* completely digesting a full blood meal in 72 hours would do so at an average rate of 0.11 mg. amino acids released per mg. midgut tissue per hour. The maximum *in vitro* rates secured with blood and serum albumin as substrates are 17.3% and 47%, respectively, of this. The abnormal physical state of the blood and the

[18] *See* Note 14, page 565.

reduced midgut: substrate ratio which obtained during the experiments are possibly responsible for the apparent inefficiency of the tests.

8. Feeding experiments undertaken to discover some relatively simple property or properties of blood which enable it to pass directly to the midgut while other fluids go first to the diverticula were negative. Certain of the hypotheses regarding this interesting "switching mechanism" are discussed critically.

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EXPERIMENTAL DESIGNS, by WILLIAM G. COCHRAN and GERTRUDE M. COX. ix+454 pp. London, John Wiley & Sons, Inc. Chapman & Hall, Limited. 1950. Price $5.75.

The subject of experimental designs and statistical analysis of research data has become of utmost importance in our research investigations. The authors have written the book as a manual to aid researchers in planning and evaluating their scientific investigations. References to additional statistical information for each chapter are listed.

In the first two chapters, the relationships of statistics to the experiments and to the methods of increasing accuracy are discussed. In this portion of the book experimenters are shown the value of planning their work so it can be analyzed. The analysis of field data is becoming an integral part in our investigational work and essential in presenting the results. In chapter 3 the techniques of statistics in mathematical design are outlined.

Many types of designs used in actual experimental work are explained in chapters 4 through 13. The advantages and limitations of each design are presented. Experimental designs discussed and exemplified are: complete randomization, randomized blocks, latin squares, factorials, split-plot designs, quasi-latin squares, incomplete blocks, lattices and cubic lattices, balanced incomplete blocks, lattice squares and incomplete latin squares. Plans and examples of experimental designs are copious and are one of the very desirable features of this book. In chapter 15, tables of random permutations for 9 and 16 allow for numerous random arrangements.

The treatise, although not completely suitable for workers without some knowledge in statistics, does give (pp. 1–38) an excellent and logical background of the value of statistics and how they can be used by experimenters. The authors should be commended on the presentation of experimental designs so that the book can be used as a manual by many research workers.

—LOYD L. STITT AND JOHN F. MOORE.

A QUALITATIVE ANALYSIS OF THE FREE AMINO ACIDS IN INSECT BLOOD[1]

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The free amino acid content of the blood of insects is strikingly high in comparison with that of other animals. It varies from 40 mg.% in adults and young larvae to as high as 385. mg. % in some mature larvae and in pupae (3, 5, 7, 11, 12, 13, 16, 17, 22, 29). Comparable values for the blood of decapod Crustacea are from 1.6 to 8 mg. % (23) and for whole human blood 6 mg. % (14).

Relatively little is known of the quality or quantity of the individual amino compounds which comprise this high level of amino nitrogen. Ranga-Rao and Screenivasaya (26) found 2.5% free tyrosine in the water soluble portion of the body fluids of the lac insect *Lakshadia mysorensis*. Florkin and Duchateau-Bosson (17) identified histidine and tyrosine in the blood of adults of the beetle *Dytiscus marginalis* and obtained negative tests for arginine, cysteine, cystine, phenylalanine, and tryptophane. Ussing (28, 29) recorded the first occurrence of asparagine in animal blood when he isolated this amide from the blood of larvae of *Melolontha vulgaris*. He also found arginine, histidine, leucine, lysine, tryptophane, tyrosine, valine, and probably hydroxyproline and glutamine in this species and all these except asparagine in the blood of *Oryctes nasicornis*.

Raper and Shaw (27) found alanine, glycine, leucine or isoleucine, proline, serine, tyrosine, valine, and possible arginine and lysine in the blood of nymphs of the dragon-fly, *Aeschna cyanea*. Finlayson and Hamer (15) found the above amino acids and also identified aspartic acid, histidine, isoleucine, lysine, and phenylalanine in the blood of *Calliphora erythrocephala* larvae.

EXPERIMENTAL

Amino Nitrogen Determinations

In order to obtain data concerning the quantity of blood required for amino acid analysis, the free amino nitrogen of the blood of three species was determined. Amino nitrogen was measured by the submicro method of Van Slyke, MacFadyen and Hamilton (30). An all glass apparatus was used in order to avoid the possibilities of inaccuracies due to rubber connections (30). Determinations were made on the

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whole blood of larvae of *Apis mellifera* and *Galleria mellonella*, and adults of *Blatella germanica*. Aliquots of 50 microliters from pooled samples of heat-treated blood were used for all determinations. The results are presented in Table I.

Qualitative Analysis of Amino Acids

Qualitative separation and identification of the free amino acids and certain amino acid derivatives in insect blood was accomplished by the paper partition chromatographic method of Consden, Gordon and Martin (6). The technique used was essentially that described by Dent (10). All separations were carried out in two dimensions on 18 by 22.5 inch sheets of Whatman No. 1 filter paper, using phenol and a 1:1 mixture of gamma-collidine and 2, 4-lutidine as solvents. The phenol was allowed to flow over the paper for 26 to 30 hours and the collidine-lutidine for 60 hours. After revealing the positions of the amino acids by spraying the paper with a 0.1% solution of ninhydrin in

TABLE I

AMINO NITROGEN CONTENT OF THE BLOOD OF THREE SPECIES OF INSECTS

Species	Amino Nitrogen (Mg./%)
Apis mellifera (worker larva)	164.9
Galleria mellonella (larva)	199.4
Blatella germanica (adult)	56.4

n-butanol and heating in an oven at 100° C. for 10 minutes, the chromatograms were read by placing them over the diffusion plate of an X-ray illuminator (24).

Reference chromatograms were made of all of the naturally-occurring amino acids and of several other amino compounds. Methionine was revealed as its sulfoxide or sulfone and cystine as cysteic acid by oxidation of the sample with H_2O_2 as described by Dent (10). Leucine and isoleucine were not completely separable with the solvents used but definition of these compounds was obtained by a second separation in collidine-lutidine for 48 to 60 hours in a direction opposite to that of the phenol separation.

Pooled samples of whole blood were diluted with 10 times their volume of 95% ethyl alcohol (8) and the precipitated proteins removed by centrifugation. The precipitate was washed three or four times with a few microliters of alcohol in order to extract completely the free amino acids. The alcohol extract was evaporated to a volume of approximately 25 microliters by a jet of air, oxidized for methionine and cystine conversion, then placed on the filter paper for separation. Blood samples of 25, 50, 100 and, in some instances 200 microliters were analyzed for each species whenever possible.

Amino acids and other ninhydrin-reacting compounds separated from blood samples were identified by comparing blood chromatograms

with previously prepared chromatograms of pure amino acids. Positive identification of doubtful compounds was made by preparing two chromatograms from the blood sample: one of the blood alone and one to which a few micrograms of the suspected compound was added. Coincidence of the spot of the suspected compound with that of the pure compound added to the blood sample verified the identification.

In early analyses it was necessary to verify the suspected presence of glutamine and asparagine in blood samples. This was accomplished by subjecting the sample to mild hydrolysis with 6 N HCl. The absence of spots in the positions occupied by these amides on the developed chromatogram, in addition to some intensification of the glutamic and aspartic acid spots, confirmed the identification.

The free amino acids and other ninhydrin-reacting compounds identified in the blood of the seven species studied are listed in Table II.

DISCUSSION

Amino Nitrogen

The value of 164.9 mg.% of amino nitrogen in the blood of larvae of *Apis mellifera* is considerably lower than the average value of 288 mg.% reported by Bishop *et al.* (5). This difference may be attributable to normal variation in amino nitrogen content of the blood, for Ussing (29) found differences as great as 170 mg. % in the blood of *Melolontha vulgaris* larvae. Taurine also contributes to amino nitrogen measurements in some methods and may help account for the higher value of Bishop *et al.* (5) since the present study shows considerable free taurine in the blood of bee larvae.

The value of 199.4 mg.% of amino nitrogen in the blood of *Galleria mellonella* larvae agrees with published values for other lepidopterous species (3, 11, 12, 13, 22). Considerably less amino nitrogen (56.4 mg.%) was present in adults of *Blatella germanica* than was found in the larval species. Smaller quantities of amino nitrogen in the blood of adults than in that of larvae have been found in other species (13, 16, 17).

Blood extracts containing approximately 100 micrograms of amino nitrogen were found to yield chromatograms of optimum separation and definition of the amino acids present, although complete analyses could be accomplished with 50 micrograms of amino nitrogen. Approximately 200 micrograms was found to be the maximum quantity of amino nitrogen which would give clearly defined chromatograms of the amino acids in a blood sample.

Free Amino Acids

In the following discussion reference will occasionally be made to the relative quantities of some of the amino acids present in the blood of certain species. Quantitative estimates are only approximate and were based on the size and intensity of the chromatographic spot and on the sensitivity data of Pratt and Auclair (24).

It is apparent from Table II that the amino nitrogen of insect blood is composed of a wide variety of amino acids and their derivatives. Alanine, glutamic acid, glutamine, glycine, isoleucine or leucine,

TABLE II

FREE AMINO ACIDS PRESENT IN THE BLOOD OF SEVEN SPECIES OF INSECTS

Amino Acid or Derivative	*Blatella germanica* Adult	*Periplaneta americana* Adult	*Musca domestica*		*Oncopeltus fasciatus* Adult	*Prodenia eridania* Larva	*Galleria mellonella* Larva	*Apis mellifera* Larva		
			Adult	Larva				Worker	Drone	Queen
Alanine	+	+	+	+	+	+	+	+	+	+
Arginine	+	–	–	+	–	+	+	+	+	+
Aspartic acid	+	–	+	+	+	+	+	+	+	+
Cystine	+	+	+	–	+	+	+	+	+	+
Glutamic acid	+	+	+	+	+	+	+	+	+	+
Glycine	+	+	+	+	+	+	+	+	+	+
Histidine	?	–	–	–	–	+	+	–	–	+
Hydroxyproline	–	–	–	–	–	–	–	+	+	+
Isoleucine and/or Leucine	+	+	+	+	+	+	+	+	+	+
Lysine	+	–	+	–	+	+	+	+	+	+
Methionine	+	+	+	+	+	+	+	+	+	+
Phenylalanine	–	–	+	+	–	+	–	–	–	–
Proline	+	+	+	+	+	+	+	+	+	+
Serine	+	+	+	+	+	+	+	+	+	+
Threonine	+	–	+	–	–	+	+	+	+	+
Tryptophane	–	–	–	–	–	?	+	+	+	+
Tyrosine	+	+	+	+	+	+	+	+	+	+
Valine	+	+	+	+	+	+	+	+	+	+
β-Alanine	+	–	+	–	+	+	+	+	+	+
α-Amino-n-butyric acid	–	–	–	–	–	+	+	–	–	+
Asparagine	+	–	–	–	–	+	+	+	+	+
Glutamine	+	+	+	+	+	+	+	+	+	+
Taurine	–	–	+	+	+	–	–	+	+	+

+ Identified in one or more blood samples.
? Questionable identification in one or more blood samples.
– Not identified in any blood samples.

methionine, proline, serine, tyrosine, and valine were present in the blood of all species and occurred consistently in all blood samples analyzed. Occurring in smaller quantities and less consistently encountered in blood samples were α-amino-n-butyric acid, β-alanine, arginine, asparagine, aspartic acid, cystine, histidine, hydroxyproline, lysine, phenylalanine, taurine, threonine, and tryptophane. Histidine is the least sensitive of the amino acids to the ninhydrin reaction after separation on filter paper (10, 24), which may account for the failure to detect this compound in the blood of some of the species.

Histidine was not identified in blood samples of *Blatella germanica* but was found in water extracts of individual adults from which the digestive tract had been removed. Although Auclair (1) has shown that the tissues of most of the internal organs of *B. germanica* do not contain sufficient quantities of free amino acids to detect by paper partition chromatography, it is possible that the histidine may have been due to contamination by gut contents during preparation or to free histidine in tissues of the integument.

Hydroxyproline was identified only in the blood of larvae of *Apis mellifera*. The blood of queen larvae contained less than the blood of worker and drone larvae. An indication of the probable source of hydroxyproline in the blood of bee larvae is apparent in the work of Auclair and Jamieson (2) who showed that significant quantities of free hydroxyproline were present in a mixture of several species of pollen collected from a bee hive. It is generally accepted that the food of worker and drone larvae consists largely of pollen after the first two days of their feeding period, whereas queen larvae are fed solely on royal jelly. Pratt and House (25) were unable to find hydroxyproline in royal jelly, either free or as a protein constituent. Contamination of royal jelly with small quantities of pollen may explain the presence of hydroxyproline in the blood of queen bee larvae.

The spots of leucine and isoleucine coincide on two-dimensional chromatograms when phenol and collidine-lutidine are used as solvents, but partial separation occasionally occurs. Careful comparisons of chromatograms showing some separation of leucine and isoleucine with standard chromatograms indicate that both of these compounds are probably present in all the species studied. Positive identification of leucine and isoleucine in the blood of larvae of *Prodenia eridania* and *Galleria mellonella* was accomplished by separation in three directions, as described above. Finlayson and Hamer (15) recently identified both leucine and isoleucine in the blood of *Calliphora erythrocephala* larvae by two-dimensional chromatography using phenol and benzyl alcohol as solvents.

The presence in insect blood of certain amino acids other than those which are known protein constituents is of interest to studies on the metabolism of nitrogenous compounds by insects.

β-Alanine, which was found in the blood of all species except adults of *Periplaneta americana* and larvae of *Musca domestica*, occurs in vertebrate tissues in combination with histidine in the peptides carnosine and anserine (4) but these compounds are not known to be present in invertebrate tissues (21). Dent (10) detected β-alanine in plant tissues, thus indicating that it is available to animals in their food. Auclair (1)

found that *l*-cystine is responsible, directly or indirectly, for the formation of β-alanine in *Blatella germanica*. Since β-alanine is a constituent of pantothenic acid, which is required by some insect species for growth (18, 19, 20), it may arise as a metabolic product of this vitamin.

α-Amino-n-butyric acid was identified in the blood of larvae of *Prodenia eridania*, *Galleria mellonella*, and queen larvae of *Apis mellifera*. Dent (8, 9) has shown that this amino acid is present in human blood and urine and can be formed metabolically from methionine. Auclair (1) found that *Blatella germanica* can also metabolize methionine to α-amino-n-butyric acid.

The presence of asparagine in the blood of four of the species studied is especially interesting, for it had not been detected in the blood or tissues of animals until recently when Ussing (28, 29) isolated the compound from the blood of *Melolontha vulgaris* larvae. Insects apparently obtain asparagine from plants where it occurs widely and parallels the function of glutamine in animal blood by serving as a storage compound for ammonia (4).

Glutamine was present in the blood of all species studied. It is an important metabolite in both plants and animals, where it functions in ammonia storage and metabolism. Ussing (29) has pointed out that glutamine may function in uric acid synthesis in insects since it has been demonstrated that the rate of uric acid formation by bird liver slices increases upon the addition of glutamine.

Taurine was found in relatively large quantities in the blood of *Musca domestica* larvae and adults, *Apis mellifera* larvae, and *Oncopeltus fasciatus* adults. High concentrations of taurine have been found in muscle tissue of certain invertebrates and smaller quantities are present in vertebrate muscle (4), but the presence of this compound in insect blood or tissues has not previously been reported. Dent (10) identified taurine in human blood and urine. The function of taurine as a constituent of vertebrate bile salts is well known but its function as a free compound in animal tissues is unknown (4). A study of the metabolism of taurine by insects might reveal information concerning their bile function.

The ability of insects, particularly during the larval stage, to store large quantities of free amino acids in the blood invites speculation as to the purposes and mechanisms of such storage. Amino nitrogen studies on holometabolous insects by other workers indicate that blood amino acids increase in quantity as the larva grows (12), remain high during pupation (7, 17, 22), then decrease somewhat in the adult (7, 11, 17). It is of interest that the amino nitrogen content of pupae is little, if any, greater than that of the blood of mature larvae (5, 7, 13, 17). These observations substantiate the suggestion of Ussing (29) that amino acids stored by the larva may be used for protein synthesis during metamorphosis. Deaminating enzymes must be absent or inactive to account for the progressive increase of amino nitrogen during larval development and for its maintenance at a high level during pupation. It is not known whether there are any quantitative changes in the amino nitrogen content of the blood of adults with aging or in the blood of hemimetabolous insects during development.

SUMMARY

1. The free amino nitrogen content of the blood of three species of insects was determined and the following quantities found: *Apis mellifera* larvae, 164.9 mg.%; *Galleria mellonella* larvae, 199.4 mg.%; *Blatella germanica* adults, 56.4 mg.%.

2. The free amino acids present in the blood of seven species of insects were analyzed qualitatively by means of paper partition chromatography. The amino acids and derivatives found present in the blood of all the species were: alanine, glutamic acid, glutamine, glycine, leucine or isoleucine, methionine, proline, serine, tyrosine, and valine. Those found present in only certain of the species were: β-alanine, α-amino-n-butyric acid, arginine, aspartic acid, asparagine, cystine, histidine, hydroxyproline, lysine, phenylalanine, taurine, threonine, and tryptophane.

3. The possible sources and metabolic significance of some of the amino acids found in insect blood are discussed.

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ERRATUM

The passage on page 406, third paragraph, lines 8 and 9, beginning with the word "*Phlebotomus*," should read: "*Phlebotomus* was found on eight occasions and at all elevations. A total of 176 . . ." instead of "*Phlebotomus* was found at thirteen localities in six different parishes at elevations." The latter passage occurs in the previous paragraph, lines 3 and 4, in its correct context.

NOTES ON THE FORM OF DISTRIBUTION OF INSECT AND PLANT POPULATIONS

F. M. WADLEY

PROBLEMS INVOLVED

Many population studies result in figures of number of organisms per unit, as per square foot or per plant. The frequency distributions involved are of interest, for what they can tell us of the tendencies of the organisms concerned, and for light they shed on proper statistical analysis.

It is easy to show that if a population distributes itself over a number of units at random, the distribution of numbers per unit will approximate a Poisson series. Deviation from a Poisson will indicate failure of randomness. Experience shows that there is nearly always a departure from the Poisson, in the direction of greater dispersion and higher variance. There is an excess of zeros and high values over Poisson expectation. This indicates unequal probability among units of receiving organisms. Sparse populations often come near the Poisson; denser ones usually diverge more from it. Variance is equal to the mean in the Poisson; comparison of variance and mean is a test for divergence.

Some mathematical distributions have been fitted with allowance for the divergence. If one distribution is consistently successful, it may be supposed to give a mathematical picture of the divergence. Fisher (1941) has recently called attention to the negative binomial of the form $(q-p)^{-k}$, where $q=1+p$, and k is positive. Neyman (1939) and Beall (1940) have fitted contagious distributions involving a compounding of simple random tendencies. Fracker and Brischle (1944) advanced the idea that a mixture of Poisson and contagious distributions might explain some natural distributions.

A suitable transformation for analysis of population values may be suggested by the distribution (see Cochran 1938, Beall 1942). The square root transformation is suited for Poisson data; the logarithm of $(n+1)$ is better for the divergent distributions usually found. Beall (*l.c.*) has tabled a transformation suited to the degree of divergence found, passing from the square root toward the logarithmic. In some cases a special transformation may be derived from a specific problem. The proper transformation will give a distribution nearer the normal and will stabilize variance.

However, in many cases in practice, the total number of organisms per set of units, or per experimental treatment, is sufficient to give an approach to normal in successive samples. All these distributions tend to approach the normal as numbers increase. For this reason, and because analytical procedures give fairly good results in slightly skew distributions, transformations may be dispensed with in many cases.

These distributions have been fitted to a number of population counts. In some cases the figures are from uniformity counts in solid

areas; in others, from sample counts scattered over their areas. In either case, counts will reflect the distribution tendencies.

METHODS USED

The first cases studied are of organisms of Ribes bushes in forest; this is the material studied by Fracker and Brischle (*l.c.*). In a typical case, 80 units of 1/10 acre each are enumerated, with results as follows:

Bushes per unit	0	1	2	3	4	5	above 5
Frequency	43	15	8	6	3	4	1

In the "above 5" class was one area with 13 bushes. There were 94 bushes on the 80 areas, with mean 1.18 and variance 3.89.

The Poisson series, standard of randomness, can easily be fitted. The general term for proportion of units with a given number, X, is: $\frac{e^{-\overline{X}} \cdot \overline{X}^x}{X!}$

(Here $\overline{X}$ is the mean and X! is "factorial X"). In fact, the terms of a Poisson have been tabled by Pearson (1930, Table 51) for various means at intervals of 0.1. In the above case, the expected Poisson frequencies for a mean of 1.18 are about 24, 29, 17, 7, 2, and 1, respectively, for values of 0, 1, 2, 3, 4, 5. There is plainly a wide discrepancy; the variance 3.89, greatly exceeding the mean, 1.18, is enough to indicate this.

Neyman's "Contagious distribution" in its simpler form (Type A, 2 parameters) is next fitted. The expected proportion of units with zero is first calculated; successive terms are then figured from the preceding ones. The relation of the mean ($\overline{X}$) and variance (V) is used to calculate constants; $m_1 = \overline{X}^2/(V-\overline{X})$: $m_2 = (V-\overline{X})/\overline{X}$. The expression for proportion of zeros is: $P_o = e^{-m1\ (1-e^{-m2})}$. The general expression for terms other than zero is:

$$P_{(n+1)} = [\ (m_1 \cdot m_2 \cdot e^{-m2})/(n+1)]\ \cdot\ S^n_{k=o}\ [m_2{}^k/k!\ \cdot\ P_{(n-k)}]$$

For the case cited above, with V = 3.89 and $\overline{X}$ = 1.18:

$m_1 = (1.18)^2/(3.89-1.18) = 0.514$

$m_2 = (3.89-1.18)/1.18 = 2.297$

e^{-m_2} = antilog $(-m_2 \times \log e)$ = antilog (-2.297×0.4343) = antilog (-0.9976) = 0.1006

$1-e^{-m_2} = 0.8994$

$-m_1\ (1-e^{-m_2}) = (-0.514 \times 0.8994) = -0.4623$

$e^{-m_1\ (1-e^{-m_2})} = e^{-0.4263}$ = antilog (-0.4623×0.4343) = antilog $(-0.2008) = 0.6298$

Since $P_o = 0.63$ about, the expected number (F_o) is 80 x 0.63 or 50.4.

For P_1 we have: $[\ (m_1 \cdot m_2 \cdot e^{-m_2}]/1]\ \cdot\ [\ (m^o{}_2/0!)\ P_o]$

0! is factorial 0, equal to 1)

or $[\ (0.514 \times 2.297 \times 0.1006)/]\ \times 1/1)\ (0.63) = 0.0748$

F_1 is 80 x 0.0748 or 6.0

For P_2 the expression is $[\ (m_1\ m_2\ e^{-m_2})/2]\ [\ (m^o{}_2/0!)\ (P_1) + m^1{}_2/1!)\ (P_o)\ ]$

which gives us 0.0902; F_2 is estimated as 7.2

For P_3 we have: $[\ (m_1\ m_2\ e^{-m_2})/3]\ [\ (m_2{}^o/0!)\ (P_2) + m_2{}^1/1!)\ (P_1) + (m_2/2!)\ (P_o)]$

This is solved as 0.0760, with $F_3 = 6.1$

Succeeding frequencies are solved in the same way as 4.2, 2.6 and 3.5; for 4, 5 and all above 5 respectively. The last figure is secured by subtraction.

The negative binomial has the general term:

$P^x = q^{-k} \cdot [(k+X-1)!/X!(k-1)!] \cdot (p/q)^X$;

Where k is $\overline{X}^2/(V-\overline{X})$, and p is $(V-\overline{X})/\overline{X}$ (the same as m_1 and m_2 of the contagious distribution) and $q = 1+P$.

In the present example $k = 0.514$, $p = 2.297$, $q = 3.297$.

For P_o the expression reduces to q^{-k}, or

$P_o = 3.297^{-0.514} =$ antilog $(-0.514 \times \log 3.297) =$ antilog $(\bar{1}.2663) = 0.542$

$F_o = 80 \times P_o = 43.4$

$P_1 = 0.542\ [0.514!/(1!-0.486!)]\ (2.297/3.297)^1$.

To solve this, (0.514)! and (−0.486)!, must be secured from a table of factorials such as Pearson's (*l.c.*, Table 31). When this is done, the expression becomes:

$0.542 \times 0.887/1.726 \times 0.6967 = 0.1941$, and

$F_1 = 0.1941 \times 80$, or 15.5,

$P_2 = 0.542\ [1.514!/2\ (-0.486)!]\ (0.6957)^2 = 0.1023$, and

$F_2 = 8.2$.

In the same way, frequencies for 3, 4, 5 and above 5 are estimated as 4.8, 2.9, 1.8 and 3.4 respectively.

The three distributions fitted can now be compared with actual frequencies.

TABLE I

Distribution	Units Having							Chi-square
	0	1	2	3	4	5	6 and up	
Poisson	24.6	29.0	17.0	6.7	2.0	0.5	0.2	35.8** (3)
Contagious	50.4	6.0	7.2	6.1	4.2	2.6	3.5	17.6** (4)
Negative binomial	43.4	15.5	8.2	4.8	2.9	1.8	3.4	4.7 (4)
Actual	43	15	8	6	3	4	1	.....

Chi-square for the Poisson is computed by lumping small classes to give an expected frequency over 1 in the smallest class. This leaves 5 classes (24.6, 29.0, 17.0, 6.7, 2.7). A degree of freedom is deducted for the mean and one for the total number, leaving 3 degrees of freedom. Chi-square is computed as $S[(O-C)^2/C]$, where C is the calculated and O the observed number in each class. The other two distributions have 7 classes, all with expected frequencies over 1; but 3 deductions must be made, for mean, variance and total number, since both mean and variance are used in fitting.

The number of degrees of freedom follows each chi-square in parenthesis. An asterisk indicates significance at the 5% point, 2 asterisks show significance beyond the 1% point. The high chi-square for the Poisson shows marked divergence of the actual counts from Poisson theory. The chi-square for the contagious distribution is lower but still significant. Other forms of the contagious distribution might be tried, but Beall (*l.c.*) shows that all give rather similar results.

The chi-square for the negative binomial is low, well in line with expectation, and shows that the sample could easily be from a distribution of this sort.

RESULTS WITH SEVERAL POPULATION COUNTS

The methods outlined have been tried on several other *Ribes* counts, on some counts of wireworm larvae in soil secured through the kindness of E. W. Jones (see Jones 1937), and on two Japanese beetle larval counts. The results are shown in Tables II, III, and IV. For each analysis is shown the total number, mean, variance, and chi-squares for the Poisson, contagious and negative binomial distributions.

Results of the *Ribes* counts are shown in Table II. They are for tenth-acre units unless otherwise specified. The counts are from solid areas, and in some cases were of remaining or new bushes some time after a cleanup operation. Variances are relatively high and the

TABLE II

RIBES DISTRIBUTION COMPARED WITH THEORY

AREA	N	$\overline{X}$	V	CHI-SQUARE FOR		
				Poisson	Contagious	Negative Binomial
Kaniksu	80	1.18	3.89	35.8** (3)	17.6** (4)	4.7 (4)
Cow Creek	100	2.96	19.80	265.7** (7)	410.4** (6)	11.9 (6)
Mt. Spokane	64	1.22	12.30	52.1** (3)	539.3** (1)	8.1* (2)
Clearwater	64	1.52	8.92	77.2** (4)	165.1** (4)	0.3 (4)
Beaver Creek	400	1.06	3.05	251.4** (4)	35.8** (3)	1.0 (3)
" " (sq. rds.)	6,400	0.0662	0.1004	237.0** (1)	14.0** (2)	0.6 (3)

counts give a severe test to distributions. The Beaver Creek data were also available by square rods, as shown. Because of the large numbers these would be expected to show high chi-squares, but the fit of both compound distributions was fair or good. This data was also available by acres, with $n=40$, $\overline{X}=10.60$, $V=74.72$. It showed a broad, flat distribution, impossible to fit reasonably by Poisson or contagious, but preliminary trials showed the negative binomial as giving promise of a fair fit.

The wireworm distributions are from sample units scattered over their area. Units were ¼ to 1/16 square foot. Variance is not high in most cases. In a few cases of low mean and variance, distributions were not calculated, since they were close to Poisson expectation, and classes were too few to test the other distributions. This omission applied to all cases with means below 0.50, and one with mean 0.89.

Lastly, two distributions of Japanese beetle larvae in soil were fitted. The counts are of larvae per square foot, in solid areas, and were from the material described by Fleming and Baker (1936). The two

sparser populations were used. The higher populations showed distributions approaching symmetry, and offered considerable difficulty in arithmetic because of the number of terms.

It is easy for divergence from any distribution to appear, because of the large numbers involved. In one case Fisher's suggestion of using the maximum likelihood fitting was explored for the negative binomial. It offered only a small improvement.

TABLE III

WIREWORM DISTRIBUTIONS COMPARED WITH THEORY

N	$\bar{X}$	V	CHI-SQUARE FOR		
			Poisson	Contagious	Negative Binomial
100	0.77	1.17	10.6* (3)	5.2* (1)	4.4 (2)
100	0.90	1.30	10.4* (3)	9.2* (3)	6.7* (2)
100	1.94	3.31	32.0** (5)	2.4 (4)	2.5 (4)
101	2.64	15.73	140.8** (6)	509.2** (6)	15.6 (9)
100	0.50	1.10	14.3** (2)	2.6 (2)	1.6 (3)
100	0.64	0.98	3.9 (2)	2.5 (2)	1.1 (2)
100	0.73	0.78	4.5 (2)	5.6 (1)	2.8 (1)
100	0.83	1.76	15.5** (2)	6.2 (3)	0.8 (4)
100	0.88	1.10	4.7 (3)	0.4 (2)	0.2 (2)
100	1.13	1.97	15.6** (3)	9.9* (4)	5.5 (4)
99	2.05	5.96	30.1** (5)	17.9* (7)	6.9 (7)
198	2.83	7.54	162.1** (7)	14.2 (8)	3.8 (9)

TABLE IV

JAPANESE BEETLE GRUB POPULATIONS COMPARED WITH THEORY

N	$\bar{X}$	V	CHI-SQUARE FOR		
			Poisson	Contagious	Negative Binomial
2500	2.76	5.88	781.3** (7)	149.6** (10)	62.8** (10)
2500	5.14	12.27	3100.5** (14)	94.2** (15)	36.8** (15)

DISCUSSION AND CONCLUSION

First it may be noted that the negative binomial as used was practically always better than the Poisson or the form used of the contagious distribution. The latter was usually, but not always, better than the Poisson. Furthermore, the distributions usually did not show significant departure from the negative binomial, and usually did show significant departures from the other two.

Next the distributions may be divided into those showing little excess of variance over mean, moderate excess, and great excess. Where variance was not over 150% of the mean, the Poisson might give a

fairly satisfactory fit. With variance from 1½ to 3 times the mean, the contagious distribution and the negative binomial both surpassed the Poisson, and the advantage of the latter over the former was not great. In the several extreme cases, with variance 6 to 10 times the mean, the contagious distribution was even worse than the Poisson, and the negative binomial still gave a fairly good fit.

As previously stated m_1 (or k) is calculated as $\bar{X}^2/(V-\bar{X})$, m_2 (or p) as $(V-\bar{X})/\bar{X}$. Where the variance greatly exceeds the mean, m_2 or p is large, and m_1 or k is moderate in size. Where the variance approaches the mean, k becomes large and p small. With variance equaling the mean (Poisson condition), p will be zero. In long series it may be seen that each frequency of the negative binomial is fitted as the product of a constant term, a middle term first increasing and then decreasing, and a third term decreasing as a power of a fraction. With the contagious distribution each frequency is fitted as the product of a decreasing first term, and a compound term first increasing, then decreasing.

In the cases where the negative binomial is markedly better than the contagious distribution, the superiority of fit has usually been in the first few terms; zeros, ones, twos, etc. The negative binomial expression for zero frequency is evidently a better representation of actual conditions than that of the contagious distribution. (Compare q^{-k}, or in Neyman's notation $(1+m_2)^{-m1}$ with Neyman's $e^{-m1\,(1-e^{-m2})}$.

It seems likely that the negative binomial will give in general a better representation of actual population distributions than the contagious distribution. This may be tentatively connected with the assumptions involved. In both the parameter used for the simple Poisson is assumed to vary. The "contagious" assumes discontinuous variation of this parameter. The negative binomial assumes continuous variation of the type shown by Eulerian curves. The latter assumption seems to fit bitter the factors governing population distributions.

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LIST OF THE APHIDIDAE OF THE MALAY PENINSULA, WITH DESCRIPTIONS OF NEW SPECIES

(HOMOPTERA)

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The aphid fauna of the Malay Peninsula has not been thoroughly explored and about 17 species of these insects have been recorded from the Peninsula, including Singapore, by van der Goot, Corbett, Takahashi and others. In this paper a list is given of 68 species and subspecies now known to occur on the Peninsula, of which 15 are described as new to science.

All the specimens were collected by the author unless otherwise stated and all of them, including the types, were deposited in the Selangor Museum, Kuala Lumpur.

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Cervaphis cambodiensis Takahashi

Host plant, *Grewia tomentosa*; attacking the lower side of young leaf.

Kuala Lumpur: very common, sometimes occurring in large numbers, but no alate form was detected.

Hitherto known from Cambodia, French Indo-China (Govt. Agr. Res. Inst. Formosa, Rept. No. 78, p. 9, 1941).

Setaphis viridis van der Goot

Host plant, *Glochidion* sp.; attacking the young branch.

Kuala Lumpur (31.XII.1942). Previously recorded from Johore (Philippine Jl. Sc., 21: 422, 1922).

Neophyllaphis podocarpi Takahashi

Host plants, *Podocarpus* spp., attacking the young leaf.

Kuala Lumpur: apterous forms (20.VII.1943; 22.VII.1944); Rampang, the Riouw Islands (I.1946).

Paratrichosiphum roepkei van der Goot

Host plant, *Euyra* sp.?

Singapore (Tijdschr. v. Ent., 60: 115, 1918). Not collected by the author.

Greenidea anonae Pergande

Host plant, *Baccaurea motleyana* ? attacking the lower side of young leaf.

Kuala Lumpur: many apterous forms and a few nymphs of alate form attended by *Oecophylla smaragdina* (18.IV.1943).

Greenidea ficicola Takahashi

Host plant, *Ficus* sp.; attacking the lower side of leaf.

Cameron Highlands (5000 ft.): many apterous forms (24.IX.1944).

Body mostly brownish black on the dorsum, shining; head yellowish brown; cornicles blackish brown, darker apically. The specimens differ from the Formosan ones in color.

Greenidea hirsuta n. sp.

Apterous viviparous female.—Brownish black, with the head and thorax pale greenish brown. Cornicles blackish brown, darker on the distal half. Body with many long stout setae, which are mostly branched at the tip and curved. Head a little protruding widely on the front, frontal setae somewhat longer than the basal antennal segment. Frontal tubercles absent. Antennae slender; the third

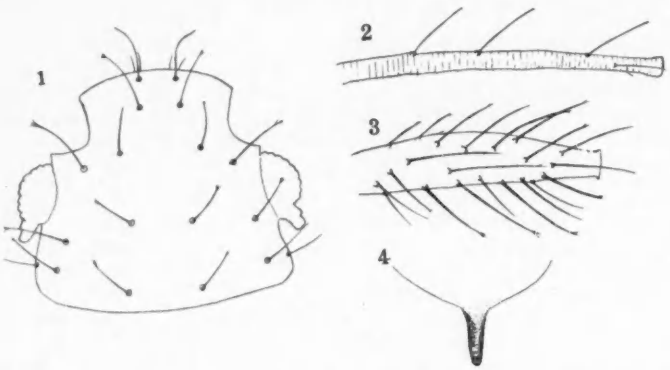

FIG. 1. *Greenidea hirsuta* n. sp., apterous viviparous female: (1) head and pronotum, (2) third antennal segment, (3) cornicle, (4) cauda.

segment a little striate, about 1.8 times as long as the fourth, with 4 long setae and some smaller ones, which are blunt at the tip; the fifth a little longer than the fourth, with two similar long setae and a shorter one; the sixth with the basal part nearly as long as the fifth; the distal part somewhat longer than the third, twice or slightly over twice as long as the basal part. Abdomen subcircular, sclerotized on the dorsum; the setae stout, dark, longer than those on the head. Minute granules present on the venters of thorax and basal part of abdomen. Cornicles about five times as long as wide, a little narrowed towards the base on the basal part, narrowest at the apex, longer than the femur, with a few translucent striae at the base, with spinules almost over the whole surface, with many long dark bristles, which are a little longer than those on the abdomen, and some of which are branched apically. Cauda with a slender process. Anal plate with numerous simple bristles which reach beyond the caudal process. Tibiae indistinctly a little striate.

Body 1.75 mm. Antenna 1.8 mm. Cornicle 0.6 mm. Abdomen 1 mm. wide.

Host plant, an undetermined tree.

Cameron Highlands (5000 ft.): many apterous forms (1.X.1944).

This species has a long caudal process like *G. schimae* Takah. from Formosa, but is different from that species in the color, and in the blunt setae on the antennae, as well as in other characters; and is distinguished from *G. decaspermi* Takah. by the shorter cornicles and other structures.

Eutrichosiphum lithocarpi malayense n. subsp.

Apterous viviparous female.—Black, brownish on the head; cornicles black. Body widened on the abdomen, with many long bristles, some of which are branched at the tip. Head a little protruding at the middle part of front, slightly concave at the middle of the protuberance; frontal setae longer than the basal antennal segment. Frontal tubercles short. Antennae much shorter than the body, five-segmented; the third segment a little striate, a little shorter than the fourth and fifth together, with over 15 long setae; the fourth nearly as long as the basal part of the fifth, with about 4 long setae; distal part of the fifth about twice as long as the basal part. Abdomen rounded at the side, sclerotized on the dorsum, with granules on the lateral part of venter; indistinct, more minute granules also present on the dorsum. Cornicles rather stout, about five times as long as wide, rounded on one side, broadest at the middle part, narrowest at the apex, lacking reticulations, with spinules over the whole surface, with many very long setae, which are longer than those on the body. Caudal segment rounded. Tibiae not striate, with many simple setae, some of which are longer than the width of tibia; fore tibiae a little longer and wider than the third antennal segment; hind tibiae longer than the cornicle.

Body 1.5 mm. Antenna 0.75 mm. Cornicle 0.45 mm.

Alate viviparous female.—Black, cornicles and stigma black. The third antennal segment nearly as long as the fourth and fifth taken together, with about 18 long setae, and about 20 large, transversely oval sensoria in a row over the whole length; the fourth a little longer than the basal part of the fifth, with about four long setae; distal part of the fifth about twice as long as the basal part, much shorter than the third. Cornicles long, moderately swollen on the distal half, narrowest at the apex, nearly as long as the hind tibia, much longer than the third antennal segment, faintly striate on the basal part, with spinules on the distal part, with many very long bristles, which are much longer than those on the body. Caudal segment rounded. Legs slender; tibiae not striate, with many long fine setae; fore tibiae a little longer than, but nearly as stout as, the third antennal segment.

Body 1.5 mm. Antenna 1.2 mm. Cornicle 0.65 mm.

Host plant, *Quercus* sp.: attacking the young leaf and shoot.

Cameron Highlands (5000 ft.): many apterous and a few alate forms (1.X.1944).

Different from *E. lithocarpi* Maki in possessing branched bristles on the body.

Greenideoida vandermeermohri Takahashi

Alate viviparous female.—Mostly pale greenish white, a little dusky on the head, pro- and mesonota, and on the dorsum of abdomen. Eyes red. Antennae, cornicles, wing veins and stigma black. Body narrow, with setae scarcely or not capitate. Front ocellus ventral. Antennae slender, imbricated, five-segmented; the third segment long, somewhat shorter than the fourth and fifth together, with 4 to 9 circular sensoria in a row on the basal half, which are variable in size; the fourth nearly as long as the basal part of the fifth, without secondary sensoria; the fifth with an oval primary sensorium at the base of the distal part, which is slightly longer than the basal part. Abdomen with minute spinules in short transverse rows on the dorsum. Fore wings narrow, a little dusky at the end of radial sector, imbricated on the marginal area; media obsolete at the basal part, once branched; radial sector somewhat curved; stigma rather slender, pointed apically; hind wings small, narrow, imbricated, with no oblique veins. Cornicles long, slender, cylindrical, striate. Legs slender. Other structures similar to the apterous form.

Body 1.7 mm. Antenna 1.6 mm. Cornicle 1.5 mm.

Host plant, *Bridelia* sp.; attacking the lower side of leaf along the rib.

Kepong, Selangor: many apterous and a few alate forms in small colonies (28.VI.1944).

Previously only the apterous form is recorded from Sumatra (Miscell. Zool. Sumatr., 97, p. 1, 1935).

Greenideoida mesuae n. sp.

Apterous viviparous female.—Yellow, greenish yellow, or almost blackish green. Cornicles dusky yellowish brown, or black, pale on the distal part. Body elongate, a little rounded on the side of abdomen, broadest at the middle of abdomen. Head almost straight or slightly convex at the middle of front, on the dorsum with four simple setae between the eyes, and with two pairs of longer setae on the front, which are blunt at the tip and somewhat shorter than the basal antennal segment. Frontal tubercles very short, indistinct, with a seta on the mesal side. Eyes rather small, protruding, with distinct ocular tubercles. Antennae long, slender, striate, as long as, or shorter than, the body, five- or six-segmented; the third segment long, nearly as stout as the tibia, somewhat longer than the fourth, fifth and the basal part of the sixth taken together in six-segmented ones, but nearly as long as the fourth and fifth taken together and much longer than the fore tibia in five-segmented ones, with over 25 setae, the longer ones of which setae are slightly longer than the width of the segment; the fourth as long as the fifth or the basal part of the sixth, with about nine setae; distal part of the sixth about 1.5 times or twice as long as the basal part. Prothorax fused with the head, narrower than the mesothorax. Abdomen with many granules on both surfaces, a few stiff dorsal setae in rows, and with about 15 stiff simple setae on the side, which are nearly as long as those on the front; basal and distal abdominal segments defined. Cornicles long, slender, shorter than the antenna, a

little curved, striate, distinctly narrowed towards the apex, with many minute spinules in rows on the apical part, with many simple setae except on the basal part, the longer ones of which setae are nearly as long as the largest diameter of the cornicle. Caudal segment somewhat triangular, rounded apically, with some long setae. Legs slender; trochanters defined; femora narrower than the cornicle; tibiae distinctly striate, without stout setae at the apex; tarsi with about five setae on the basal segment.

Body 2–2.1 mm. long, 0.9 mm. wide. Antenna 1.5–2.1 mm. Cornicle 1–1.6 mm.

Alate viviparous female.—Yellow, black on the head, antennae and mesothorax, with a very wide black band at the middle of abdomen. Eyes dark red. Cornicles black, but whitish apically. Legs dusky, brownish in specimens in balsam. Wings slightly clouded along the first oblique and stigmatic vein; veins and stigma black. Body elongate. Head straight on the front, with some stiff setae, which are very slightly capitate and shorter than the basal antennal segment, and four of which are near the hind margin of the dorsum. Frontal tubercles absent. Antennae six-segmented; the third segment a little tapering, striate, stouter than the tibia, much longer than the fourth and fifth together, slightly longer than the fore tibia, with 23 to 30 transversely oval sensoria in a row along the whole length, and with over 25 stiff setae, which are nearly as long as, or a little shorter than, the diameter of the basal part of the segment; the fourth slender, as long as the fifth, with 2 to 5 small oval sensoria in a row about the middle part; basal part of the sixth a little shorter than the fifth; the distal part a little over twice as long as the basal part. Abdomen with a few short setae in rows. Cornicles very long, cylindrical, somewhat tapering on the distal half, slightly curved, stouter than the femur, much longer than the tibia, a little shorter than the antenna, not reticulate, with many setae except on the basal part, which are nearly as long as the diameter of the basal part. Caudal segment rounded. Legs slender; hind tibiae striate, with many short setae. Fore wings imbricated narrowly along the margin; subcosta with 4 to 6 pores in a row about the middle; the second oblique a little curved; the third once branched, more slender than other oblique veins, obsolete at the basal part; stigmatic vein slightly curved, reaching the tip of the wing; stigma not reaching near the tip; hind wings small, with no oblique, hooklets 3 or 4.

Body 2.1 mm. Antenna 2.1 mm. Cornicle 1.9 mm. Fore wing 2.35 mm.

Host plant, *Mesua ferrea*; attacking the young leaf and branch.

Kuala Lumpur: common, sometimes found in large numbers, being visited by Oecophylla smaragdina.

Related to *G. ceyloniae* van der Goot, but differs from the brief original description of that species in the apterous form wanting capitate setae, and in the alate form with 23 to 30 sensoria on the third antennal segment, and in other characters.

Aiceona osugii Takahashi

Host plant, *Actinodaphne* sp.?; attacking the young leaf.

Kuala Lumpur (Bukit Nanas): common.

Previously known from Mt. Ari, Formosa (Dept. Agr., Govt. Res. Inst. Formosa, Rept. No. 10, p. 76, 1924).

Readily differentiated from *A. actinodaphnis* Takah. and *A. siamensis* Takah. by the presence of more sensoria on the antennae in the alate form and by the pale greenish yellow apterous form.

Nippolachnus pyri Matsumura

Host plant, *Pyrus granulosa*.

Cameron Highlands (5000 ft.): some apterous forms (6.X.1944).

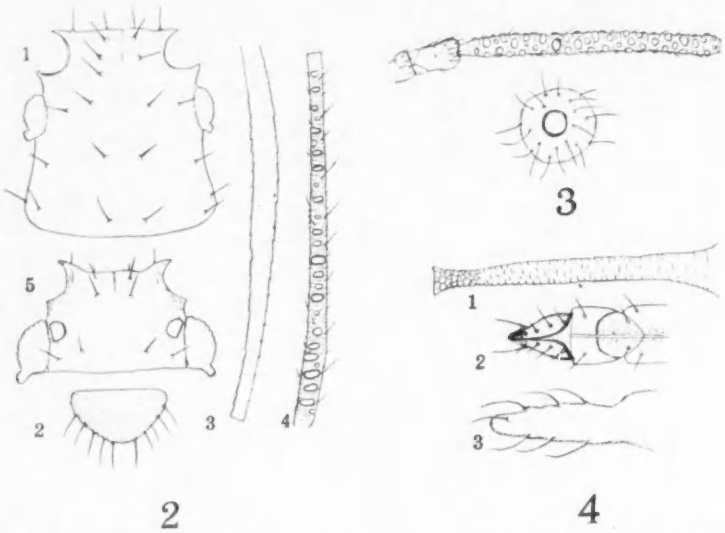

FIG. 2. *Greenideoidea mesuae* n. sp. Apterous viviparous female: (1) Head and pronotum, (2) cauda, (3) cornicle (outline). Alate viviparous female: (4) third antennal segment, (5) head.

FIG. 3. *Aiceona osugii* Takah. Alate viviparous female: third antennal segment and cornicle.

FIG. 4. *Sitobion avenae graminis* n. subsp. Apterous viviparous female: (1) Cornicle, (2) distal part of rostrum, (3) cauda.

Lachnus tropicalis van der Goot

Host plant, *Quercus* sp.; attacking the branch.

Cameron Highlands (5000 ft.): some apterous and alate forms (1.X.1944).

Macrosiphum ibarae Matsumura

Host plant, *Rosa* sp.

Fraser's Hills, Pahan: a few apterous forms (6.VI.1943).

Macrosiphoniella sanborni Gillette

Host plant, Chrysanthemum.

Cameron Highlands (5000 ft.): a few apterous form (26.IX.1944).

Macrosiphoniella yomogifoliae Shinji

Host plant, *Artemisia* sp.
Cameron Highlands (5000 ft.): some apterous forms (1.X.1944).
Different from *M. artemisiae* Boyer in the fewer setae of the cauda.

Sitobion avenae graminis n. subsp.

Apterous viviparous female.—Blackish, slightly with a powder. Dorsum sclerotized, or with many sclerites; antesiphuncular and postsiphuncular sclerites distinct, the latter more developed; a pair of sclerites present at the median area and a lateral one larger, with 2 setae. Dorsal setae short, much shorter and fewer than the ventral ones, stiff, blunt at the tip, in rows. Head slightly protruding at the middle part of front. Antennae black; the third segment not imbricated, with 1 to 3 small sensoria near the base; antennal setae short, as in the typical form. Distal segment of rostrum longer than wide, a little rounded on the side of the basal half, slightly concave on the side of the distal half, a little shorter than the penultimate segment, much shorter than the second tarsal segment. Cornicles slender, reticulate at the distal one-fifth or less, about 1.5 times as long as the cauda, with no distinct flange at the tip, black. Cauda normal in shape, black, with 3 pairs of lateral setae and an apical one. Tibial setae stiff, shorter than the width of tibia; tarsi with 3 spine-like setae on the basal segment.

Body 2.2–2.4 mm. Antennae about 3 mm Cornicle 0.55 mm. Hind tibia 1.5 mm.

Host plant, a species of the Gramineae; attacking the flower stalk.
Cameron Highlands (5000 ft.): some apterous forms (2.X.1944).
Differs from the typical form in the black cauda.

Dactynotus cameronensis n. sp.

Apterous viviparous female.—Black; antennae, cornicles and cauda black. Legs pale brown on the basal halves of femora and tibiae, black on the remaining parts. Many small subcircular sclerites present at the bases of dorsal setae; postsiphuncular sclerites large. Head not imbricated, with 4 simple setae in a row between the eyes, and a pair between the posterior parts of frontal tubercles, which setae are stiff or a little curved and much shorter than the second antennal segment. Frontal tubercles developed, normal. Antennae long, slender, with some setae which are as long as, or shorter than, the width of third segment; the third segment nearly as long as the fourth and fifth taken together, not imbricated, with about 20 setae and about 25 very small circular sensoria scattered mostly on the basal half or two-thirds except at the base; the fourth somewhat imbricated, equal in length to the fifth, about thrice as long as the basal part of the sixth; distal part of the sixth shorter than the third. Rostrum reaching beyond the hind coxae; distal segment slender, a little tapering, subequal in length to the penultimate. Cornicles cylindrical, rather stout, widened towards the base on the basal half or third, nearly as long as the third antennal segment, much longer than the cauda, imbricated, reticulate on the distal fourth. Abdomen with many setae in rows. Cauda normal in shape, constricted near the basal part, with about 15 setae. Legs long,

slender, with many stiff setae; tibiae stouter than the third antennal segment; hind tibiae narrowed distally, with stiff setae which are mostly shorter than the width of tibiae, tarsi normal.

Body 2.5 mm. Antennae 3.3 mm. Cornicle 1.0 mm.

Alate viviparous female.—The third antennal segment with about 60 small sensoria scattered over the whole length except at the basal and distal small parts; the fourth without sensoria. Cornicles widened towards the base on the basal part. Other characters as in the apterous form.

Host plant, a large plant of the Compositae.

Cameron Highlands (5000 ft.): some apterous forms and an alate form (29.IX.1944).

Closely related to *D. gobonis* Matsumura, differing, however, in the third antennal segment with fewer sensoria, which are scattered mostly on the basal half or two-thirds in the apterous form, as well as in the simple setae on the body. Differentiated from *D. taraxaci* Kalt. by the presence of a distinct postsiphuncular sclerite; from *D. solidaginis* Fab. by the longer third antennal segment; and from *D. jaceae* L. by the fewer setae on the cauda, the distal part of the sixth antennal segment being much shorter than the third, and by other characters. Also different from *D. lactucicola* Strand from Formosa in the presence of more sensoria on the antennae in the apterous form and in some other structures.

Dactynotus compositae Theobald

Host plant, a plant of the Compositae.

Kluang, Johore: common (XI.1945).

Myzus circumflexum Buckton

Host plant, *Wormia* sp.?

Cameron Highlands (5000 ft.): 2 apterous forms (1.X.1944).

Myzus sp.

Host plant, a composite.

Cameron Highlands (5000 ft.): some nymphs (26.IX.1944).

Probably *M. persicae* Sulzer.

Megoura citricola van der Goot

Host plant, *Cinnamomum* sp.

Singapore (Tidjschr. v. Ent., 60: 115, 1918,). Not collected by the author.

Megoura simplocois van der Goot

Host plant, an undetermined tree.

Cameron Highlands (5000 ft.): a few apterous forms (24.IX.1944).

Closely resembles *M. citricola* van der Goot, but differs in the cauda with 3 pairs of lateral setae.

Micromyzus nigrum van der Goot

Host plant, Maidenhair fern.

Singapore (Corbett and Gater, Dept. Agr. Fed. Malay St., Bull. No. 38, p. 6, 1926). Not collected by the author.

Pentalonia nigronervosa Coquerel

Host plants, banana, *Alpinia* sp., *Caladium*.

Kuala Lumpur, Sungei Buhlo, Setapah, Selangor: common, but occurring in small colonies.

Rhopalosiphum maidis Fitch

Host plant, corn.

Recorded from Malaya by Corbett and Gater (Dept. Agr. Fed. Malay St., Bull. No. 38, p. 6, 1926), but not found by the author.

Hyalopterus arundinis Fabricius

Host plant, *Phragmites* sp.

Kuala Lumpur, Sungei Besi, Selangor: common.

Brachysiphoniella graminis Takahashi

Host plant, *Leersia* sp.

Malacca: many apterous forms and an alate form (12.VIII.1943); Kuala Sleh, Selangor: many apterous form (18.IV.1944).

Toxoptera aurantii Boyer

Host plants, Mangosteen, *Thea*, *Citrus*, *Artocarpus integrifolia*, *Ficus pumila*, a composite, etc.

Singapore; Kuala Lumpur, Kepong, Dusun Tua, Ulu Gombak, Selanger; Fraser's Hills, Cameron Highlands: common, sometimes attended by *Oecophylla smaragdina* or *Crematogaster* sp.

Toxoptera citricida Kirkaldy

Host plant, *Citrus*.

Kuala Lumpur: some apterous and alate forms (2.I.1943).

Very closely related to *T. aurantii* Boyer, with peculiar sculptures on the abdomen, and should be included in this genus, though the media of fore wings is usually twice branched as in *Aphis*.

Aphis gossypii Glover

Host plants, *Hibiscus rosa-sinensis*, cotton, *Melastoma* sp., *Colocasia*, *Solanum* spp., *Jacaranda mimosaefolia*, a composite.

Kuala Lumpur; Telakanson, Krian, Perak; Fraesr's Hills, Cameron Highlands; Rempang, Riouw Islands: common.

Aphis malvoides van der Goot

Host plant, a composite (*Bidens* ?).

Singapore, Kuala Lumpur: common.

Aphis glycines Matsumura

Host plant, soy bean.

Puchong, Selangor: many apterous and a few alate forms (25.VII.1944).

Aphis laburni Kaltenbach

Host plants, Beans.

Kuala Lumpur, Dusun Tua, Selangor: common.

Previously recorded from Johore as *A. medicaginis* Koch (Philippine Jl. Sc., 21: 421, 1922).

Aphis nerii Boyer

Host plant, *Asclepias crassavica.*

Singapore: a few specimens collected by Corbett and Gater (19.XII.1925).

Aphis saliceti Kaltenbach

Host plant, *Salix tetrasperma.*

Dusun Tua, Selangor: many yellowish apterous forms and an alate form (23.V.1943).

Some of the apterous forms are provided with small sensoria chiefly on the distal half of the third antennal segment and may be regarded as intermediate forms between the alate and apterous females.

Aphis odinae van der Goot

Host plant, *Cinchona.*

Cameron Highlands (5000 ft.): a few apterous forms (II.XI.1943).

Aphis sacchari Zehntner

Host plants, sugar cane, sorghum.

Kuala Lumpur, Gombak, Kuala Selanger: common.

Aphis bambusae Fullaway

Host plant, bamboo.

Singapore, Kuala Lumpur, Lawan, Selangor; Krian, Perak: common, but occurring in small numbers.

Aphis pahanensis n. sp.

Apterous viviparous female.—Brownish purple; antennae pale brown, darker at the apices of segments; legs mostly pale brown. In specimens treated with potash, dorsum without patches, cornicles and cauda pale brown. Body and its appendages with much white cottony wax in life. Body normal in shape, with long fine setae. Head smooth on the surface, not protruding at the front, with setae longer than the basal antennal segment. Frontal tubercles absent. Antennae slender, six-segmented, with many long fine setae which are shorter than the fourth segment; the third segment a little imbricated, a little narrower and much shorter than the fore tibia, nearly as long as, or somewhat shorter than, the fourth and fifth taken together, without sensoria, with about 15 long fine setae; the fourth as long as the fifth, with about 5 similar setae; basal part of the sixth a little shorter than the fifth, as long as the tarsus; the distal part nearly as long as the third, 2.5 times as long as the basal part. Rostrum short, stout, reaching the middle coxae; the distal segment longer than wide, tapering, pointed, nearly as long as the penultimate. Abdomen with setae in irregular rows on the dorsum, about 4 setae present between the cornicles. Cornicles short, as long as the cauda, somewhat widened towards the base, about twice as long as wide at the apex, nearly as wide as the femur, as long as, or a little longer than, the dorsal setae of abdomen, scarcely or not striate, with no flange distinct. Cauda a little tapering rounded at the apex slightly constricted, with 5 or 6 setae. Tibiae slender with many long fine setae.

Body 1.25 mm. Antennae 0.77 mm. Hind tibia 0.5 mm.

Host plant, a plant of the Gramineae resembling *Arundinaria*; attacking the lower side of leaf.

Cameron Highlands (5000 ft.), Pahan: some apterous forms (26.IX.1944).

Closely related to *A. arundinariae* Takah. but differs in the body being provided with much cottony wax, the dorsum without patches at the bases of setae, the cornicles with no apical flange, the six-segmented antennae, with the distal part of the last segment being as long as the third, the shorter setae on the body and antennae and in other characters.

Oregma bambusae Buckton

Host plant, bamboo: attacking the young shoot and the lower side of young branch.

Kuala Lumpur: sometimes occurring in large numbers, attended by *Dolichoderus*.

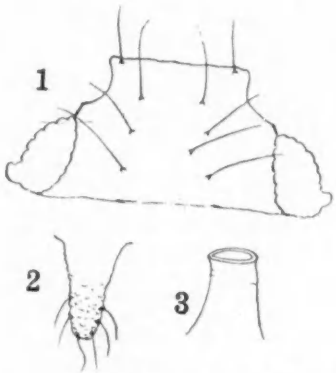

FIG. 5. *Aphis pahanensis* n. sp. Apterous viviparous female: (1) head, (2) cauda, (3) cornicle.

Oregma pendleburyi n. sp.

Apterous viviparous female.—Dorsum sclerotized over the whole surface, with numerous granules. Frontal horns distinctly diverging, tapering, but rounded at the tip, as long as, or slightly longer than, the basal antennal segment. Antennae four- or five-segmented. Thoracic and basal six abdominal segments each sometimes with 1 to 4 small oval wax-pores on the dorsum, the eighth abdominal tergite sometimes with 3 to 5 small wax-pores in a group at the middle. Cornicles small.

Body 2.7 mm.

Host plant, bamboo.

Kedah Peak (3000 ft.): many apterous forms collected by H. M. Pendlebury (15.III.1928).

Differs from *O. bambusae* Buckton in the whole dorsum being sclerotized and in the smaller cornicles, as well as in the first stage nymph with granules over the whole dorsum, with longer horns and with

the fore femora being much swollen. Distinguished from *O. sundanica* van der Goot by the larger body, and by the distal segment of rostrum being stouter, a little longer than wide and usually a little rounded on the side.

Oregma gombakana n. sp.

Apterous viviparous female.—Blackish brown, somewhat purplish, with small patches of wax along the side and on the dorsum. Body oval, stout, convex dorsally, distinctly sclerotized on the whole dorsum, slightly granular on the anterior part of dorsum. Head and prothorax

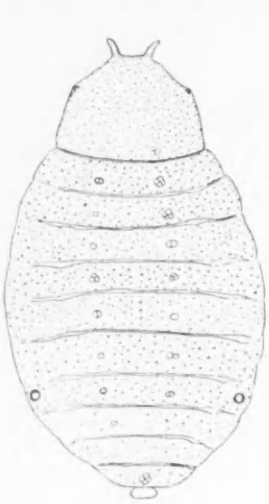

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FIG. 6. *Oregma pendleburyi* n. sp. Apterous viviparous female.

FIG. 7. *Oregma gombakana* n. sp. Apterous viviparous female. Body and cephalo-prothorax.

with some groups of areolations on the dorsum, which are much smaller than the wax-pore and about 3 to 14 in number in each group. Frontal horns longer than wide, diverging, as long as the basal antennal segment, bluntly pointed or rounded at the tip. Eyes of three facets Antennae nearly as long as the fore femur, four-segmented; the third segment widened distally, with a few short setae; the fourth a little shorter than the third, shorter than the fore tarsus. Distal segment of rostrum stout, nearly parallel on the sides, rounded at the side of apex, pointed at the middle of apex, longer than wide, a little shorter than the penultimate segment. Abdominal segments distinct, with some rather short stiff setae in a row; the seventh tergite with 3 setae; the eighth with a pair of setae, between which a group of wax-pores is located.

Cornicles small, smaller than the wax-pore. Cauda short, much constricted basally, with about 8 long setae along the hind margin, of which 2 at the middle are much longer. Anal plate deeply bilobed, with 7 or 8 setae on each lobe. Legs rather short and stout; femora with many faint areolations; tibiae with some fine setae which are shorter than the width of tibia; tarsi slightly striate, the basal segment with 2 median and 2 similar, but longer, lateral setae in the fore pair, with a median and 2 longer lateral setae in the middle pair, and with only a pair of long setae in the hind pair. Wax-pores large, but sometimes small or scarcely developed, in a compact group on the side and in a pair of groups on the dorsum of each segment, but the seventh abdominal tergite with no dorsal group and the eighth with a median dorsal group only; numbers of wax-pores in each group about as follows: (dorsal group) 1 to 7, usually 4 to 6, on thorax, 2 to 7 on abdomen, but 3 to 8 on the eighth segment, (lateral group) 5 or 6 on thorax, 3 to 5 on abdomen.

Body 1.7–1.8 mm.

Host plant, bamboo: attacking the basal part of the upper side of leaf.

Ulu Gombak, Sungei Tua Selangor: some apterous forms in small colonies (17.IV., 11.V., 18.VII.1944).

Distinguished from *O. bambusae* by the dorsum sclerotized over the whole surface, with large wax-pores, and by other characters, and from *O. sundanica* van der Goot by the presence of wax-pores on the dorsum. Different from *O. montana* van der Goot in the colour, the fewer wax-pores which are larger than the cornicle, and in other structures.

Oregma sundanica van der Goot

Host plants, a plant of the Zingiberaceae, *Amomum*.

Singapore; Ulu Gombak, Kepong, Selangor; Fraser's Hills: common, sometimes occurring in large colonies.

Oregma nicolaiae Takahashi

Host plant, *Elattaria cardamomum*.

Kuala Lumpur (Insecta Matsumurana, 15, p. 149, 1949). Not collected by the author.

Trichoregma nipae van der Goot

Host plants, *Zalacca*, coconut palm, *Elaeis*, Nipah palm.

Singapore; Sunegi Buhlo, Klang, Ulu Gombak, Kuala Lumpur, Kuala Selangor, Selangor; Fraser's Hills: common, sometimes occurring in large colonies.

Trichoregma muiri van der Goot

Host plants, *Amomum*, *Languas*.

Singapore, Fraser's Hills.

Trichoregma musae Takahashi

Host plant, a plant of the Zingiberaceae.

Sungei Buhlo, Serdang, Damansara, Ulu Gombak, Selangor: common.

Different from the Sumatran specimens in the fewer (5 or 6) setae on the cone of cornicle and in the wax-pores on the head and thorax being narrower and closely arranged in rows.

Trichoregma singaporensis van der Goot

Host plant, bamboo.

Singapore: many apterous forms (2.III.1944).

Trichoregma rhapidis van der Goot

Host plants, *Cocos*, *Elaeus*, *Kentia*, *Calamus* sp.

Singapore; Kuala Lumpur, Ulu Gombak, Selangor: many apterous and some alate forms (II. and IV.1944).

Trichoregma malaccensis n. sp.

Apterous viviparous female.—Dark purplish brown, with much wax along the body margin. Body oval. Head and prothorax fused together, with about 20 long fine dorsal setae, which are as long as, or a little longer than, the frontal horns. Horns pointed, a little diverging, rather slender, as long as, or slightly longer than, the basal antennal segment. Eyes protruding. Antennae four-segmented; the third segment a little longer than the fourth, narrowed towards the base, often with a distinct constriction near the base, with about 3 setae on the distal half; the fourth with 2 setae on the basal part. Distal segment of rostrum short, a little widened towards the base, somewhat shorter than the penultimate segment. Abdomen not so widened, slightly sclerotized around the bases of setae on the dorsum, with 2 setae between the rows of wax-pores on the sixth and seventh tergites, but with 4 setae in a row between the cornicles on the fifth; the eighth a little sclerotized, with the rows of wax-pores very closely placed, a pair of setae at the middle in front of the pores, and with 2 lateral setae at the hind margin. Wax-pores large, arranged in an irregular row on the side of each segment, oval or irregularly narrowed in shape, mostly larger than the cauda; those on the sixth and seventh abdominal segments sometimes a little larger, those on the sixth located transversely behind the cornicles; numbers of wax-pores in each row about as follows: 2 to 5 on head, 3 or 4 on porthorax, 3 on mesothorax, 3 or 4 on metathorax, 3 on basal abdominal segment, 4 on second to seventh, 4 to 6 on eighth. Cornicles separated from the rows of wax-pores, with 2 setae on the cone. Cauda constricted basally, with about 9 long setae. Anal plate divided. Legs with some long fine setae; tibiae stouter than the third antennal segment; tarsi short, with 2 long setae on the basal segment.

Body 1.0 mm.

Host plant, bamboo.

Malacca, Singapore: some apterous forms (IV.1943; V.1944).

This species is characterized by the rows of wax-pores being located transversely behind the cornicles on the sixth abdominal segment and by the third antennal segment usually with a distinct constriction near the base.

Trichoregma flava n. sp.

Apterous viviparous female.—Entirely yellow. Body oval, not so expanded on the abdomen. Head and prothorax sclerotized on the dorsum, with about 18 moderate setae; meso- and metathoraces and basal four abdominal segments each with a pair of large wide transverse sclerotized parts on the dorsum, those on the fourth abdominal segment united: the fifth to seventh each with a large transverse sclerotized part

on the dorsum; these sclerotized parts smooth, separated from the lateral ones of wax-pores. Frontal horns conical, rather stout, diverging, sharply pointed, nearly as long as the basal antennal segment. Eyes a little protruding. Antennae short, shorter than the width of head across the eyes, four-segmented; the third segment narrowed towards the base, longer than the fourth, with a few setae on the distal half; the fourth not narrowed basally, the basal part about twice as long as the distal. Abdomen with 2 to 4 short setae in a row on each tergite, sclerotized on the eighth tergite. Wax-pores large, circular or subcircular, in rows on the side only; numbers of wax-pores in a row about as follows: 1 or 2 on prothorax, 2 or 3 on meso- and metathoraces, 3 or 4 on basal seven abdominal segments, 4 or 5 on the eighth; the rows usually distinctly separated, with a pair of setae between them on the eighth. Cornicles small, low, at the apex as large as, or smaller than, the wax-pores; the cones or basal sclerotized parts separated from, or united with, the lateral sclerotized parts of wax-pores, but united with the dorsal sclerotized parts, with 1 to 4 setae. Cauda and anal plate normal. Legs short; tibiae as long as the femur and trochanter together, fore tibiae a little shorter than the antennae; fore tarsi with 4 setae on the basal segment, of which the median 2 are shorter; middle and hind tarsi with a pair of long setae on the basal segment, but the middle pair sometimes with also a median one.

Body 1.3 mm.

Host plant, bamboo: attacking the basal part of the lower side of leaf.

Taiping, Perak: many apterous forms (8.XI.1943); Malacca: a few smaller apterous forms (IV.1943).

Differs from other species of the genus in the presence of distinct sclerotized parts on the dorsum.

Trichoregma lutescens van der Goot

Host plant, bamboo.

Kuala Lumpur, Kepong, Sungei Tua, Selangor: common.

The apterous form is very variable in color, and *T. striata* van der Goot may be a form of this species.

Trichoregma salatigensis van der Goot

Host plant, bamboo.

Malacca; Tanbun near Ipoh, Perak; Dusun Tua, Selanger: many apterous forms.

Trichoregma pallida van der Goot

Host plant, bamboo.

Kuala Lumpur, Fraser's Hills: common, but usually occurring in small colonies.

Different from the Malayan specimens of *T. salatigensis* van der Goot in the presence of lateral wax-pores in rows on somewhat sclerotized parts on the thorax and abdominal segments. The aphid recorded as *T. salatigensis* van der Goot from Siam (Govt. Agr. Res. Inst. Formosa, Rept. No. 78, p. 16, 1941) may be this species.

Ceratovacuna lanigera Zehntner

Host plants, sugar cane, *Saccharum arundinaceum*.

Kuala Lumpur, Serdang, Batu Caves, Selanger, Cameron Highlands: common.

Cerataphis freycinetiae van der Goot

Host plant, *Freycinetia* sp.

Singapore: some apterous forms (26.V.1944).

Cerataphis lataniae Boisduval

Host plants, palms.

Kuala Lumpur, Sungei Buhlo, Ulu Gombak, Selangor: common, sometimes protected with shelters by *Crematogaster*.

Some apterous forms collected on an abnormal host, *Ficus* sp. (*Ficus fistulosa* ?) at Kuala Lumpur (7.III.1943) may represent a separate form and the description is given below.

Apterous viviparous female.—Body similar in shape and colour to that on palms. Submarginal dorsal setae nearly as long as the basal antennal segment. Frontal horns conical, pointed, expanded basally, nearly parallel on the mesal sides, slightly separated from each other at the base, almost as long as the basal antennal segent. Head on the venter with a pair of short spine-like setae between the antennae, 2 fine setae laterad of each horn, and with 2 or 3 pairs of similar setae behind the spine-like ones. Marginal wax-pores circular or subcircular, not elongate, 13 to 16 in number along the margin of the eighth abdominal tergite. Cauda with 3 pairs of setae at the hind margin, of which the last pair is much longer. Tarsi with 4 long fine setae at the apex, which are very slightly capitate; the basal segment with 2 median long stout setae and a pair of very long fine lateral setae in the fore pair, a median seta and a pair of lateral ones in the middle pair, and with only a pair of long fine ones in the hind pair.

Body 1.4–1.5 mm.

Ceratoglyphina bambusae van der Goot

Host plant, bamboo.

Kuala Lumpur (4.IV.1943), Malacca (30.IV.1943): some apterous forms.

Glyphinaphis bambusae van der Goot

Host plant, bamboo.

Singapore (Tijdschr. v. Ent., 60: 113, 1918). Not collected by the author.

Aleurodaphis blumeae van der Goot

Host plant, *Blumea* sp.

Cameron Highlands (5000 ft.): many apterous forms (IX. and X.1944).

Thoracaphis kayashimai n. sp.

Apterous viviparous female.—Closely related to *T. setigerus* Takah. (Philip. Jl. Sc., 48: 72, 1932), differing, however, in the following characters: Dorsum not reticulate, with 3 pairs of circular markings and

closely with convolute markings on the median area of thorax except on the median longitudinal narrow part, which part is not reaching the head and abdomen. Legs black; hind femora over twice as long as wide; hind tibiae a little longer than the femur, over twice as long as the tarsus; hind tarsi longer than wide, not reaching the hind end of body, somewhat narrowed on the distal half, rounded apically.

Body about 0.5 mm.

Host plant, *Quercus* sp.; attacking the lower side of leaf.

Cameron Highlands (5000 ft.): many apterous forms (1.X.1944).

Apparently different from *T. elongatus* Takah. in lacking conical spines on the median area of dorsum. Named after Mr. I. Kayashima who assisted the author's work in Malaya.

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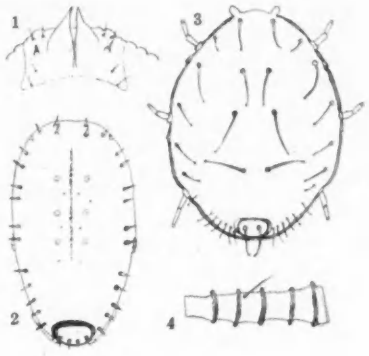

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FIG. 8. *Trichoregma flava* n. sp. Apterous viviparous female: (1) head and pronotum, (2) cornicle. *Trichoregma malaccensis* n. sp. Apterous viviparous female: (3) head and pronotum, (4) cornicle and wax-pores.

FIG. 9. *Cerataphis lataniae* Boisduval on *Ficus*. Apterous viviparous female: (1) lower side of front. *Thoracaphis kayashimai* n. sp. Apterous viviparous female: (2) dorsal view. *Thoracaphis flavus* n. sp. Apterous viviparous female: (3) dorsal view. *Astegopteryx fransseni kepongensis* n. subsp. Alate viviparous female: (4) fourth antennal segment.

Thoracaphis flavus n. sp.

Apterous viviparous female.—Pale yellowish brown, with no secretion evident. Oval, flattened, very thin, not sclerotized. Head, thorax and basal seven abdominal segments entirely fused together. Dorsum with many small, but distinct granules over the whole surface except on about 4 pairs of large oval parts on the median area and on the eighth abdominal tergite, which granules are provided with some small pointed spines; 4 pairs of long stout setae on the median area, which are capitate or narrowed on the distal part and blunt at the tip, and a pair on the head is longer than the antenna and as long as, or a little shorter than, the space between themselves; bases of these setae larger than the granules; 12 setae arranged in a row along the sub-

marginal area on each side, of which 2 posterior ones are not capitate, and 6 or 7 posterior ones are shorter and near the hind end of body; the eighth abdominal tergite separated, small, short, much wider than long, not protruding, with a pair of rather long capitate setae about the middle. Antennae horn-like, not segmented, stout, subconical, rather large, pointed apically, diverging, shorter than the femur, about 1.5 times as long as wide, marginal. Eyes not recognizable. Cornicles absent. Cauda short, wider than the anal lobe, a little constricted, with some short setae. Anal plate distinctly divided, each lobe wider than long, rounded on the margin, with some short setae. Legs exposed; hind femora over twice as long as wide; hind tibiae longer than the femur; tarsi very short, wider than long, not segmented, with 2 setae at the apex.

Body 0.5 mm.

Host plant, *Quercus* sp.; attacking the lower side of leaf.

Cameron Highlands (5000 ft.): many apterous forms (1.X.1944).

This species is characterized by the very thin flattened body, and much differs from *T. depressus* Takah. in the shape of body, the dorsum with granules and capitate setae, and in many other characters.

Thoracaphis malaynus n. sp.

Apterous viviparous female.—Black, somewhat with a brownish tinge, shining, sclerotized, with no wax evident. Body subcircular, slightly wider than long, thick, flattened on the dorsum, slightly protruding at the hind end. Cephalothorax occupying most of body, with no trace of segments, with a pair of fine setae at the anterior margin between the antennae, four transverse rows of setae on the median area (4 setae in each row), and some setae along the margin of dorsum; these setae rather or moderately long, simple, a little curved, very thin at the apical part; some minute mosaic-like markings on the lateroanterior and lateroposterior parts of dorsum. Body with a narrow rim along the whole margin on the venter. Antennae slender, somewhat shorter than the space between themselves, laid along the anterior margin of body, visible from above, basal segments not distinct, the third segment with a small sensorium at some distance from the apex. Eyes marginal, of three facets. Abdomen scarcely defined from the thorax; basal seven segments fused together, usually with a short median seta at the anterior part and, with 4 setae in a row along the lateral margin, and with a pair of setae along the hind margin; the eighth tergite separated, somewhat shorter than the basal fused part of abdomen, rounded on the margin, with 4 setae along the margin and with a very narrow rim on the lateral margin. Cornicles very small, as large as the bases of setae on the abdomen. Cauda much larger than the anal lobe, constricted, straight at the hind margin, with about 6 pairs of long fine setae on the posterior part. Anal plate deeply divided, each lobe rounded on the margin, wider than long, with about 7 fine setae on the lateral half. Legs exposed, short, with a few short fine setae; femora over twice as long as wide, slightly narrowed toward the base; tibiae longer than the femur; tarsi longer than wide, segmented, with distinct claws and thin long digitules which are not capitate.

Body 1.3 mm.

Host plant, *Quercus* sp.; attacking the branch.

Cameron Highlands (5000 ft.): some apterous form (1.X.1944).

Related to *T. machili* Takah., but differs from that species in the absence of dorsal papillae, the fewer setae, and in other structures.

Thoracaphis gooti n. sp.

Apterous viviparous female.—Black, with much white wax along the margin. Subcircular, a little longer than wide, somewhat narrower anteriorly, depressed, sclerotized, with very small irregular indentations on the margin. Thorax occupying over half the body; meso- and metanota and basal seven abdominal segments faintly discernible; abdomen not well defined from the thorax, basal two segments much longer than the following five segments, but much shorter than the thoracic segments; the eighth tergite distinctly separated, rounded on the margin, not protruding, with no marginal rim. Dorsum very roughly corrugated except on the eighth tergite, but not so distinctly, without granules; a pair of spines present near the front end and near the lateral margin of each thoracic segment; 4 similar spines between the eyes; a similar one near the lateral margin of each of basal seven abdominal segments, 4 similar ones on the eighth tergite; the spines conical, slender, pointed, short, subequal in length, very slightly narrowed at the base; thoracic and basal two abdominal segments each with a pair of simple fine setae on the median area, which are much longer than the spines and subequal in length. Eyes marginal, of three facets. Antennae on the venter, slender, as long as the space between themselves, three- or four-segmented; the fourth segment shorter than the third; the 3rd and 4th together as long as, or longer than, the fore femur. Cornicles not recognized. Cauda wider than long, somewhat constricted, with some long setae. Anal plate deeply bilobed, the lobes as long as wide, rounded, with many very long stiff setae. Genital plate large, rounded on the hind margin, as wide as the eighth tergite, sclerotized, reaching beyond the hind margin of the eighth tergite. Legs entirely concealed under the body; trochanters fused with the femora; hind legs distinctly longer, reaching the eighth tergite; hind femora as long as, or shorter than, the tibia; hind tibiae rather slender; tarsi distinctly two-segmented, with 3 setae on the basal segment, the median one of which is spine-like; tarsal digitules long, thin, knobbed; claws slender.

Body 1 mm.

Host plant, *Quercus* sp.; attacking the lower side of leaf.

Cameron Highlands (5000 ft.): many apterous forms (4.X.1944).

Named after Dr. P. van der Goot, who much contributed to the study of Aphididae of Malaysia. Related to *T. lithocarpi* Takah., but differs as follows: Dorsum not granular, with 4 spines on the eighth abdominal tergite. Dorsal setae on the median area longer than the submarginal spines. Body a little longer than wide, somewhat narrower anteriorly. Distinguished from *T. cheni* Takah. by the wider body, the cornicles wanting, the dorsum not mosaic-like on the surface, with the spines subequal in length, the distribution of spines on the head being different, and by other characters.

Astegopteryx fransseni kepongensis n. subsp.

Alate viviparous female.—Head with a pair of very short spine-like setae on the front, and with about 14 to 18 short setae on the dorsum, of which a pair near the front ocellus is sometimes longer and as long as the basal antennal segment. Front ocellus smaller than the dorsal ones, on a small protuberance. Antennae normal; the third segment slightly wider than the fore tibia; sensoria as follows: III–17–22, IV–2–6, V–0–3; setae as follows: III–4, IV–2, V–1+3 (at apex). Distal segment of rostrum about 2.2 times as long as wide, as long as or very slightly longer than and much more slender than the penultimate segment. Hind wings with 2 hooks. Four to six setae present around the cornicle. Cauda rounded with about 17 long setae. Anal plate scarcely sinuate, with 6 to 10 setae on each side. Genital plate somewhat sclerotized, with about 11 to 16 setae in a row at the hind

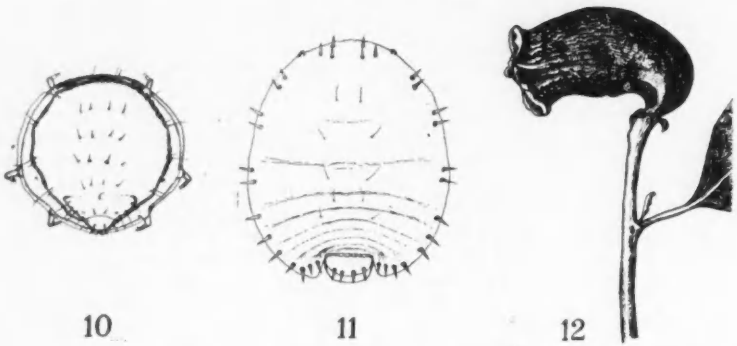

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FIG. 10. *Thoracaphis malaynus* n. sp. Apterous viviparous female: Dorsal view.

FIG. 11. *Thoracaphis gooti* n. sp. Apterous viviparous female: Dorsal view.

FIG. 12. Gall of *Astegopteryx fransseni kepongensis* n. subsp.

margin and with 3 to 5 setae at the middle part of the anterior half. Other characters as given in the description of *A. fransseni* Lambers (Miscell. Zool. Sumatra, 76, p. 2, 1933).

Host plant—*Styrax benzoin*; producing a single gall at the apex of the branch.

Kepong, Selangor: many alate forms (29.VIII.1943); Serdang, Selangor: a few alate forms (9.VI.1944).

Differs from the figure of *A. fransseni* Lambers in the antennae being slightly more slender and in the primary sensorium on the fifth antennal segment being narrower and transverse. The gall is greyish green, consisting of a single depressed bag, which is about 20–25 mm. long and 14 mm. wide, with a narrow opening at the apex.

Described from specimens from Kepong. The alate forms taken at Serdang are slightly smaller and the third antennal segment is slightly longer than the fourth and fifth taken together, with about 15 sensoria.

Tetraneura sp.

Cameron Highlands (5000 ft.): a broken alate form resting on an onion plant (11.XI.1943).

Probably identical with *T. hirsuta* Baker.

Pineus laevis Maskell

Host plant, *Pinus* sp. imported from Sumatra.

Fraser's Hills: apterous forms abundant (VI. and IX.1943).

LA BIOLOGIE DES DIPTÈRES, by E. SEGUY. Encyclopédie Entomologique (Paul Lechevalier, Paris), ser. A, xxvi. 609 pages, 10 plates, 225 text figures. 1950. 4000 francs.

This is an ambitious work, by an outstanding French authority in the field of dipterology, and it fills an important void that has existed in that field. Taxonomists have had to spend so much time in clarifying the status of the species with which they have been concerned that the biologies of most insects have had to be neglected, at least so far as a comprehensive treatment is concerned. Some notable exceptions, as in the ants, termites, mayflies, and mosquitoes, occur, but the biological information on most groups of Diptera is extremely scattered and hard to find. Monsieur Séguy's work brings together a vast amount of information into a single volume, logically treated and easy to read. An extensive list of citations is given in addition to special reference lists at the ends of chapters and sections, and an analytical index, which appears to be adequate, is appended.

Ten chapters (pp. 9–211) are devoted to the morphology (particularly internal) and physiology of the egg, larva, pupa, and adult, and to such subjects as reproduction, the hatching of the egg, and eclosion. But slight mention is made of embryology. The next nine chapters (pp. 212–470) are devoted to the ecology, geographical distribution, media (aquatic and terrestrial), and special habits and habitats (including cavernicolous, "microcavernicolous," domestic, predatory, haematophagus, and parasitic habits), of flies. A final chapter (pp. 471–527) is devoted to a brief survey and characterization of the families.

The book is worthy of the efforts of Monsieur Séguy; it is well-written, well-planned, meaty, and readable. It is accurately and artistically illustrated, and some of the color plates are particularly impressive. A large part of the preparation, however, seems to have been done prior to or during World War II, as reference to literature published since 1940 and utilization of material published in that literature is scant. The absence of many of the important recent American publications is especially notable. In general, American material seems to be treated less fully and less accurately than European: for example, the distribution of *Dermatobia* (p. 241, fig. 112) is shown as extending too far northward (well into the United States) and *Anopheles quadrimaculatus* and *punctipennis* (the latter given erroneously, instead of *freeborni*, as one of the important vectors of malaria) belong to the Sonoram subregion, as interpreted by Séguy, rather than to the Nearctic. There are other errors, but what work of this magnitude is without them?—M. T. J.

NYMPHAL MITES OF THE GENUS UROPODA ATTACHED TO A CERAMBYCID BEETLE

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On August 5, 1948, Mr. William Helps, a student at McMaster University, captured a male sawyer beetle, ***Monochamus notatus*** Drury, at Aylmer, Ontario. When examined it was seen to be covered with a mass of reddish mites which appeared to interfere in no way with its movements, since it was taken in flight and remained active when caught. The beetle was pinned and placed in a collection at McMaster University. When it was examined under a binocular microscope the following approximate counts of mites were made on various regions of the body: top of prothorax, 100; bottom of prothorax, 100; left elytron, 200; right elytron, 50; mesosternum, 50; metasternum, 55, making a total of 555 mites (fig. 1). On some areas of the body the mites were so closely crowded that they overlapped one another, some being tipped onto their edges. Each mite was attached to the integument of the beetle by a small white cord projecting from its posterior end (fig. 2). The mites were firmly attached and scraping with a needle was required to dislodge them.

Several mites were removed from the beetle and placed in preservative and were sent to Dr. H. H. J. Nesbitt of Carleton College, Ottawa, and to Dr. E. W. Baker of the Bureau of Entomology and Plant Quarantine, who kindly identified them as nymphs of the genus *Uropoda*. This assemblage of mites on the beetle is evidently a case of attachment for the purpose of transportation as described by Banks (1905), who points out that "some genera (as *Uropoda*) are chiefly known to us in this migratorial nymphal condition." The individual mite, a "nympha pedunculata," is attached to the beetle by an "anal pedicel" formed of excretions (fig. 2—AP).

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Banks, N. 1905. A treatise on the Acarina, or mites. Proc. U. S. National Museum 28(1382): 1–114.

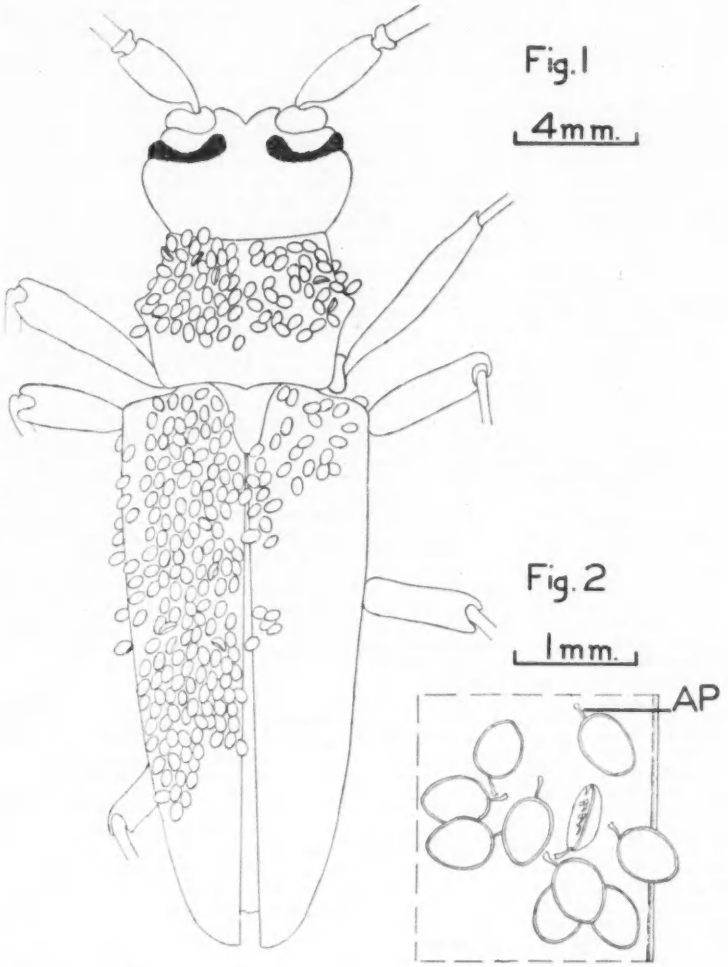

FIG. 1. Dorsal view of *Monochamus notatus* and its covering of mites.
FIG. 2. Portion of inner border of left elytron showing attached mites.
AP—anal pedicel

OBITUARIES

LELAND OSSIAN HOWARD, (1857–1950), Honorary Fellow and charter member of the Entomological Society of America, internationally known American biologist, writer and administrator, and Chief of the Bureau of Entomology, U. S. Department of Agriculture for 33 years, was born June 11th, 1857, at Rockford, Illinois. He was oldest child of Ossian Gregory Howard and Lucy Dunham [Thurber] Howard. While the child was still in infancy, the parents removed to Ithaca, New York, where the growing child later attended school. During boyhood he attended the Ithaca Academy and a Latin preparatory school. In September, 1873, he became a student at Cornell University, and during the four years that followed at that institution he not only made excellent progress with his studies, but was particularly fortunate to come under the influence of some outstanding scientists, among them Dr. Charles Valentine Riley with whom in after years he was to become very closely associated. On November 13th, 1878, Dr. Riley appointed young Howard, then newly graduated from Cornell, and age 21, to be his assistant in entomological work in Federal Agricultural service in Washington—the beginning of a period of Government connection that continued for over 49 years, and, through the subsequent work and influence of this individual, comprised one of the most important epochs thus far in American economic entomology. Dr. Riley resigned in 1879 and was succeeded for two years by Professor John Henry Comstock. At the end of that period, however, he returned to Cornell and Dr. Riley was reappointed to his former position and remained as Chief until his final resignation in June, 1894, from the then Division of Entomology. It was at that time that L. O. Howard, then age 37, was appointed to take the vacant place.

It is of profound significance that when he became Chief in 1894 the total annual appropriation for Federal entomological work of all kinds was only $30,000. When he retired from the position of Chief 33 years later in 1927 at age 70, the annual appropriation was $3,000,000. Here for once figures are eloquent and do not need to be enlarged upon. However, the story of those years is long and complex and the scope and brevity of this notice does not include more than mere mention of some of the more outstanding phases of the work performed. During the ten years that followed from 1894 to 1904, there occurred three events that fixed the attention of the whole country upon the importance of entomological work: the discovery of the gypsy moth in Massachusetts in 1889; the discovery of the San Jose scale in the United States in 1893; and the discovery of the Mexican cotton boll weevil in Texas in 1894. The research work performed on these problems was in addition to that on other insect pests being studied, and, obviously required considerable additional funds and increased personnel, and these resulted in substantial growth of every phase of the organization. In 1904 there was put into effect by Congress the plan of organization of federal entomological work by which separate units were established for investigation of pests affecting the various host plants, such as field crops, truck crops and the like, a set-up that still remains in effect at the present time in modified form in the Bureau. It was also on July 1st, 1904, that the entomological work of the Department was raised to Bureau status.

A notable addition to the striking events of the last decade of the nineteenth century was a discovery by Ross in 1898 of the carriage of malaria by Anopheles mosquito—one of the most far-reaching and revolutionary discoveries ever made up to that time in the etiology of disease, since malaria was practically a world-wide malady. Within a short time thereafter the work of Reed, Carroll, Lazear and others demonstrated that without doubt yellow fever also is mosquito-borne and is transferred only by a certain species of mosquito, and thus Medical entomology presently became a most important field of investigation and demanded intimate co-operation of the pathologists and entomologists, and in all these

Dr. Howard had an honorable part. Under his immediate supervision or in co-operation with other workers, extensive series of tests were carried on with various domestic insects in relation to disease and the results received world-wide publicity and much active discussion.

The practical use of predatory and parasitic insects in the control of injurious pests was under consideration for many years and tentative experiments had been made from very early times. Much work of this sort was carried on by Dr. Howard and his assistants, and was in some instances on extensive scale, notably that with the European and Japanese enemies of the gypsy and brown tail moths, and had a very considerable degree of success. Similar plans also were developed by him on a large scale in connection with work against the Japanese beetle, the European corn borer and others. All these and his other activities in medical entomology took him year after year on numerous and often repeated trips to Europe and other countries in course of their development.

From 1896 to 1930 Dr. Howard was recognized by being given degrees from several institutions. These included the Ph. D., M. D., LL. D., and D. Sc. More than 900 publications came from the pen of Dr. Howard during his creative years, including not only his official reports and bulletins and a veritable stream of periodical articles, but also several books. Among the more important of these were "The Insect Book," 1901; "Mosquitoes," 1901; "The House Fly," 1911; "Mosquitoes of North America," 1912–17, (4 vols., joint authorship with H. G. Dyar and Frederick Knab); "History of Applied Entomology," 1930; "The Insect Menace," 1931; and "Fighting the Insects: An Autobiography," 1933. In addition to all the activities previously mentioned, he was also identified with the following: Honorary Curator, Division of Insects, U. S. National Museum since 1895; Consulting Entomologist, U. S. Public Health Service since 1904; Senior Entomologist with grade of Senior Surgeon, Reserve of U. S. Public Health Service, since 1919; Member of Committee on Agriculture of National Council of Defense, 1917; Chairman of subcommittee on Medical Entomology, National Research Council, 1917; Trustee of Cornell University, 1900–1905; Permanent Secretary, A. A. A. S., 1898–1920—22 years; President American Association of Economic Entomologists, 1894; President of Biological Society of Washington, 1897–98; President of Cosmos Club, 1909; President of Washington Academy of Sciences, 1916; President of A. A. A. S., 1920; Honorary President of Entomological Society of Washington for many years; Vice-President International Congress of Agriculture, Paris, 1923; Honorary President International Conference of Phytopathologists and Economic Entomologists Holland, 1913; Chairman, Pan Pacific Food Conservation Congress, Honolulu, 1924; President of Section of Economic Zoology, International Congress of Zoology, Budapest, 1927; and President of International Congress of Entomology, Ithaca, N. Y., 1929. In addition to the above, he likewise was member of the following: American Philosophical Society; National Academy of Sciences; Fellow of American Academy of Arts and Sciences. He was also honorary member of many foreign scientific societies. Then too, he was decorated Chevalier Legion of Honor, (France), 1925, Officier, 1929. He was made Officier of Agricultural Merit (France) 1925, and was Medalist of the Holland Society of New York, 1924. He also received second $5,000 Capper Award and gold medal in 1931 for distinguished service in Agriculture.

Dr. Howard was married on April 28th, 1886, to Miss Marie T. Clifton of Washington. Of that union there were born three daughters: Lucy Thurber, Candace Leland (Mrs. Edward D. Payne), and Janet Moore Howard. The mother died in 1926.

His membership in the Cosmos Club, an internationally known organization of scientists, writers, artists and the like in Washington, was, as he himself has written, not only a "constant source of delight, but of the most enormous educational value." This membership beginning in 1886 continued for over sixty-four years and terminated only with his death, at which time he was the oldest member of the Club, both in years and in length of membership.

From the time of Dr. Howard's retirement in 1927 as Chief of Bureau, he served four years, until 1931, as consultant to the Department in matter concerning biological control of insect pests. He retired from Government service on June 30th, 1931, at age 74. During the 17 years that followed, he resided for a time in Washington, then moved to France, and still later he returned to America and

spent his last years in New York State. He died May 1st, 1950, at his home in Bronxville, New York. At time of death he lacked only a few weeks being 93 years of age.

Dr. Howard himself has given perhaps one of the best summations of his life when in the concluding lines of his Autobiography he says: "I have led a long and happy life, and I have been very lucky to have been able to spend it all working in entomology. Surely the world knows a great deal more today about our rivals, the insects, than it did when I was a youngster. I am thankful that fate has given me a chance to see this great progress, and to watch it from the inside, and to be one of the workers."—J. S. WADE.

HERBERT SPENCER BARBER, (1882–1950), internationally-known entomologist of the U. S. Department of Agriculture's Bureau of Entomology and Plant Quarantine, died of a heart attack on June 2 at his home, 644 6th St., N. W., Washington, D. C.

Mr. Barber's knowledge of the biology and classification of beetles had few equals. His long and broad experience in both laboratory and field was coupled with an unusual memory for details. He was an authority on weevils, leaf beetles, and seed beetles, many of which are of extreme importance to an agricultural economy.

His knowledge of entomology, and especially of entomological techniques, was so broad that many entomologists in this country made special effort to discuss their scientific studies with Mr. Barber before they were completed. Many of the younger entomologists of today owe to him much of their basic philosophy in respect to science.

Mr. Barber was born April 12, 1882, at Yankton, S. D. He was educated in the public schools of Orlando, Fla., and Washington, D.C. He met the famous coleopterist, Dr. E. A. Schwarz, while still a high school student, and in September, 1898, became a preparator of insects under Dr. Schwarz' direction. In 1902 he entered government service with the then Bureau of Entomology of the U. S. Department of Agriculture. In 1908 he was assigned to the Division of Insect Identification of the Bureau quartered at the U. S. National Museum, and served as a specialist in this Division until he died.

His interests were many and varied. He traveled and collected insects extensively in this country and in Guatemala and Mexico. He knew most of the kinds of birds, fish, flowers, shrubs, trees, and other living things in this area. Mr. Barber's interest and devotion to his chosen profession permeated his every activity and fostered an interest in all things associated with outdoor life. He made full use of every opportunity to explore the woods and streams in many sections of this country. He took special delight in sharing his knowledge and love of the outdoors with others, particularly with children, many of whom acquired through him a lifelong interest in these activities.

He was a charter member of the Entomological Society of America; and also a member of the American Association for the Advancement of Science, American Association of Economic Entomologists, Entomological Society of Washington, Washington Academy of Sciences, Biological Society of Washington, Washington Biological Field Club, and the Potomac Appalachian Trail Club.—D. G. HALL.

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